

Breeding and foraging ecology of the threatened Gould's Petrel, *Pterodroma leucoptera*

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Dedication to
the inspirational woman,
Helen Weston

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ABSTRACT

Many seabirds experience threats in their environment when breeding and foraging in the highly variable marine ecosystems. Understanding breeding and foraging ecology is crucial to conserve threatened species. The research presented in this thesis aimed to investigate the foraging ecology of Gould's Petrel (*Pterodroma leucoptera*) on Cabbage Tree Island (CTI), New South Wales (NSW), Australia, to provide a knowledge base to inform the future conservation and management of this threatened species. First, I validated my methods to ensure they were ethical and effective. I found no detectable negative impact of using tracking devices on adult mass changes and associated chick growth and breeding success. Second, I tested the reliability and practicality of four techniques (trapping adults, measuring mass change in chicks, examining images from infrared cameras and analysing temperature data from geolocators) to monitor nest attendance rates. I concluded that temperature loggers featured within geolocators could be used to monitor nest attendance effectively. Third, I explored the relationships between body mass, incubation shift duration and nest desertion and concluded that incubation success was limited by the condition of birds at the start of the shift and their tenacity to remain until relieved by their partner. Lastly, but most importantly, I identified the core foraging areas of Gould's Petrels during the breeding season, which were previously unknown. In addition, I confirmed that Gould's Petrels adopted a dual foraging strategy by measuring foraging trip durations and distances during the breeding season. Examination of regurgitated stomach contents suggested diversity and variation in diet of the Gould's Petrel, showing that it is an opportunistic forager, which is important to cope with variable environment. These findings are discussed in relation to

management of issues with a view to improving conservation strategies for this threatened species and, potentially, other small pelagic seabirds.

DECLARATION

I declare that this thesis, submitted in fulfilment of the requirement for the award of Doctor of Philosophy, in the Department of Biological Sciences, Macquarie University, is wholly my own work unless referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Yuna Kim

June 2014

ETHICS AND FUNDING DECLARATION

All work carried out for this thesis was conducted under the authorisation of appropriate ethics and scientific collection permits. All protocols and procedures were approved by the Macquarie University Animal Ethics Committee (ARA 2010/048). Research was conducted under Scientific License 101166 issued by the NSW Office of Environment and Heritage, and Banding License 8010 issued by the Australian Bird and Bat Banding Scheme.

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박사과정 하는 동안 많은 분들이 저를 위해 기도해주신것 감사합니다. 무엇보다도 늘 저를 믿고 물심양면으로 지원해주신 어머니와 아버지께 감사하고 사랑합니다. 천국에서 누구보다 저의 졸업을 기뻐하고 계실 할아버지와 기도로 늘 후원해주신 우리 할머니, 사랑합니다. 한나언니와 동생 재헌이에게도 참 고맙고 사랑합니다. 또한 나의 많은 이모들, 외삼촌과 외숙모, 경민고모와 스튜고모부께서도 끝까지 격려해주시고 사랑해주신 것 감사드립니다.

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PUBLICATIONS PRODUCED DURING MY PHD CANDIDATURE

PUBLICATIONS

Kim, Y., Priddel, D., Carlile, N., Merrick, J.R. and Harcourt, R. 2014. Do tracking tags impede breeding performance in the threatened Gould's Petrel *Pterodroma leucoptera*? *Marine Ornithology* 42: 63-68 (Chapter 2).

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Kim, Y., Priddel, D., Merrick, J.R., Carlile, N. and Harcourt, R. *In review*. Testing the reliability of direct and indirect techniques to monitor nest attendance in small seabirds. *Wildlife Research* (Chapter 3).

Kim, Y., Priddel, D. and Carlile, N. *In prep*. Incubation routine and associated changes in body mass of Gould's Petrel *Pterodroma leucoptera*. Target journal: *Emu* (Chapter 4).

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AWARDS/SCHOLARSHIP

2013–2014 International Macquarie University Research Excellence Scholarship

\$24,653 per annum for 1.212 years.

2012 Macquarie University Postgraduate Research Fund

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2011 Cumberland Bird Observers Club

\$500 provided to attend 6th International Symposium on Migratory Birds, Jeungdo, Korea.

2011 Australasian Seabirds Group

\$250 provided to attend 6th International Symposium on Migratory Birds, Jeungdo, Korea.

2011 Shinan County

\$750 provided to attend 6th International Symposium on Migratory Birds, Jeungdo, Korea.

2011 Oral presentation Student Award at Australasian Ornithological Conference – 3rd prize

2011 Stuart Leslie Bird Research Award for Conference Travel

\$990 supported to present at the Australasian Ornithological Conference from 28 September to 1 October 2011.

2011 Robert Menzies College New Member Scholarship

\$1500 provided as a fee rebate.

2011 Student Membership Award from the American Ornithologist's Union

2010 Donation of financial support for endangered species research from Lynne Joshua Fund

\$3500 provided toward tuition fees.

PREFACE

I was born on the Korean peninsula, which is rich in marine wildlife and this forged my interest in animals, particularly the movement of animals. A Master's Degree in Wildlife Conservation at Macquarie University formed the foundation of my interest in birds and the importance of bird conservation as they are confronted with threats both on land and at sea. Research on Gould's Petrel (*Pterodroma leucoptera*), the study species of my PhD, has been conducted on Cabbage Tree Island (CTI), Australia, since 1989. Its successful conservation fascinates me. When I first arrived at CTI, I was surprised by its well-harmonised research and conservation work in a natural environment. I was particularly fond of the field station (Plate 0.1) and felt like I was in a scene from the science fiction series, 'Lost'.



Plate 0.1 The igloo called “The Apple” was built in 1995. It accommodates up to three people and has shelving and storage areas.

At CTI, I was introduced to the Wedge-tailed Shearwater (my second favourite seabird) incubating between rocks near my table in the outdoor kitchen (Plate 0.2). After sunset, I could hear many birds calling and falling into the bush, some even landed on top of the igloo and would slide to the ground. At CTI, I was surrounded by many Gould's Petrels and Shearwaters. I enjoyed watching them walk awkwardly and clumsily on the ground. My curiosity kicked in, which resulted in my questioning of what these seabirds did during the day when they were at sea. I was eager to see them fly and to learn how they catch fish.



Plate 0.2 The outdoor kitchen surrounded by many natural birds' nests on Cabbage Tree Island

(©Nicholas Carlile).

From this thrilling experience at CTI, I started developing research questions for a Master's degree, which I upgraded to a PhD in 2011. My PhD research investigates the foraging ecology of Gould's Petrel. Firstly, I needed to use methods that were less invasive than standard techniques because the species is currently listed as an endangered species. Chapter 2 of this thesis investigates the impact of tracking devices. Secondly, as CTI has limited resources, I needed to work as efficiently as possible. Chapter 3 tests the validity of using different methods for monitoring parent visits. In Chapter 4, I present a study of behaviours during the incubation period using data collected by David Priddel and Nicholas Carlile. Chapter 5 presents tracking data analysis and diet study for two breeding and incubation seasons (2011 and 2012). My thesis concludes with a summary of the major findings, the conservation implications of this research, and future directions. I believe that the outcomes of my thesis contribute to the science base for identifying and mitigating threats to small seabirds. I endeavour to contribute to an international collaborative research program aimed at characterising seabird hotspots and the identification of links between this community and the wider food chain to understand marine ecosystems under stress from overexploitation and global climate change.



Plate 1.1 A pair of Gould's Petrels (©Nicholas Carlile)

In this chapter, I provide the background to this research, including a description of the study species and study sites, as well as the thesis aims and structure.

1.1 ANIMAL MOVEMENT DATA TO INFORM MANAGEMENT

Marine birds are those living in, and making their living from, the marine environment (Table 1.1). Seabirds are a subset of marine birds, and are those that truly feed at sea, either nearshore or offshore (Schreiber & Burger 2002). Concern for the survival of marine mammals and seabirds is growing (Croxall et al. 2012) because of the direct and indirect impacts of industrialised fishing (Anderson et al. 2011). In the Southern Hemisphere, the extensive and remote ranges of many species of seabirds make it difficult to monitor the effect of anthropogenic pressures on populations. However, there is evidence that many pelagic seabirds suffer high mortality due to bycatch (Trebilco et al. 2010) and are affected by other pressures such as light pollution (Reed et al. 1985). The identified impacts of fishing and other anthropogenic pressures on seabirds indicate the importance of research to enhance our understanding of their conservation biology. For example, animal movement data allows the identification of important resource areas that should be a priority for conservation.

Table 1.1 Orders of marine birds from Schreiber and Burger (2002)

| Order | Types of birds |
|-------------------|---|
| Sphenisciformes | Penguins |
| Procellariiformes | Albatrosses, petrels, storm-petrels, fulmars, shearwaters |
| Ciconiiformes | Hérons, egrets, storks, ibis, spoonbills |
| Pelecaniformes | Pelicans, frigatebirds, gannets, boobies, cormorants, anhingas |
| Charadriiformes | Shorebirds, skuas, jaegers, gulls, terns, skimmers, auks, guillemots, puffins |

The understanding of the movements of wide-ranging marine predators has been revolutionised in the last three decades due to the development of advanced tracking technologies (Egevang et al. 2010). Two forms of accurate tracking devices are platform terminal transmitters (PTT) and global positioning systems (GPS). PPT are expensive and require additional data acquisition fees and, until recently, packages were relatively heavy (>9 g; (López-López et al. 2010)). GPS have until recently been expensive and, until the development of archival technology, too heavy for deployment on smaller seabirds (>10 g; (Bouten et al. 2013)). In the last decade, smaller, lighter but less accurate, tracking devices have enabled the study of increasingly smaller species (Shaffer et al. 2006). The global location sensor (GLS) archival tag or geolocator is much lighter than either PTT or GPS, and records light levels that can be used to calculate latitude and longitude based on the day-length and timing of sunrise and sunset when integrated with an accurate clock. When the mass of the device exceeds a critical point of 3% of bird body mass, negative effects are detected (Phillips et al. 2003). Some studies (Ackerman et al. 2009; Adams et al. 2009; Paredes et al. 2005; Wanless et al. 1988) have found that even lightweight devices (0.7–3.0% of body mass) have caused reduction of body mass, offspring attendance, provisioning rates and frequency of foraging trips. These studies, however, investigated relatively large birds (>500 g). Such investigation is important not only in validating any work depends on animals behaving normally (Vandenabeele et al. 2011) but also in helping researchers move forward in ‘the three Rs’ (reduction, refinement and replacement) in wildlife research (Griffin & Gauthier 2004).

Within the broader context outlined above, the focus of this thesis is the threatened small pelagic seabird, the Gould’s Petrel (*Pterodroma leucoptera*), which breeds annually at restricted sites in south-eastern Australia.

1.2 THE LIFE HISTORY OF PETRELS

Life history theory attempts to explain different strategies in terms of ecological conditions. Petrels, as truly marine organisms, have many challenges that have played an essential role in developing different life history characteristics compared to most land birds. In general, petrels represent extreme K-selected species, characterised by high adult survival rate, high juvenile mortality and low annual reproductive output (Parry 1981). The energy-limitation hypothesis was proposed by Lack (1968) to explain seabirds' life history characteristics. Birds feeding at sea search a large area for patchily distributed food and ingested food has to be delivered to a colony that is a long distance away. Therefore, energy constraints on the ability of the parent to provide food to their chicks influence the evolution of petrels' demography. Ashmole (1963) proposed that dense aggregations of seabirds, which breed colonially, could depress local food resources, resulting in density-dependent limitations on breeding success. Additionally, petrel chicks accumulate fat during development to survive through periods when their parents cannot deliver enough food.

1.3 STUDY SPECIES AND REGION - GOULD'S PETREL

According to BirdLife Taxonomic Checklist (BirdLife International, 2014), the order Procellariiformes comprises four families: Diomedidae (albatrosses; 22 species in 4 genera), Procellariidae (petrels and shearwaters; 95 species in 16 genera), Hydrobatidae (Northern storm-petrels; 15 species in 1 genera) and Oceanitidae (Southern storm-petrels; 9 species in 5 genera). Gould's Petrel (*Pterodroma leucoptera*) has an average body mass of approximately 200 g, a body length of 30 cm, and a wingspan of 70 cm. This species is included among the gadfly petrels, which form the largest group of tube-nosed birds, with 25 species in *Pterodroma* (*Pteros*, wing; *dromos*, running = 'winged runner') (Warham 1990). *Pterodroma*

are poorly defined; current classifications are mainly based on breeding distributions, on external features like size or plumage patterns, and on skeletal features (Warham 1990). There have been reported morphological differences between *P. leucoptera* breeding on Cabbage Tree Island (CTI), New South Wales (NSW), Australia and those found in New Caledonia (De Naurois 1978). Confirming these differences, Imber and Jenkins (1981) supported the formation of a subspecies *P. l. caledonica* for the New Caledonian populations and *P. l. leucoptera* for the CTI population. In this thesis, unless otherwise noted, Gould's Petrel refers to *P. l. leucoptera* breeding principally on CTI (32°41'20"S, 152°13'29" E), 1.4 km off Port Stephens, NSW, Australia.

The breeding cycle of Gould's Petrel (Figure 1.1) is similar to many other Procellariiformes of comparable size. Gould's Petrel breeds between September and October (DEC 2006). Egg laying occurs between November and December and only a single egg is laid. During incubation, the adults alternate at the nest with one incubating the egg and fasting, whilst the other forages at sea. Incubation takes an average of 49 days. Both parents feed their chick for 13 weeks after hatching (Priddel & Carlile 2001). Their at-sea movements during the breeding season and their paths of post-breeding migration and location during the non-breeding season are largely unknown.

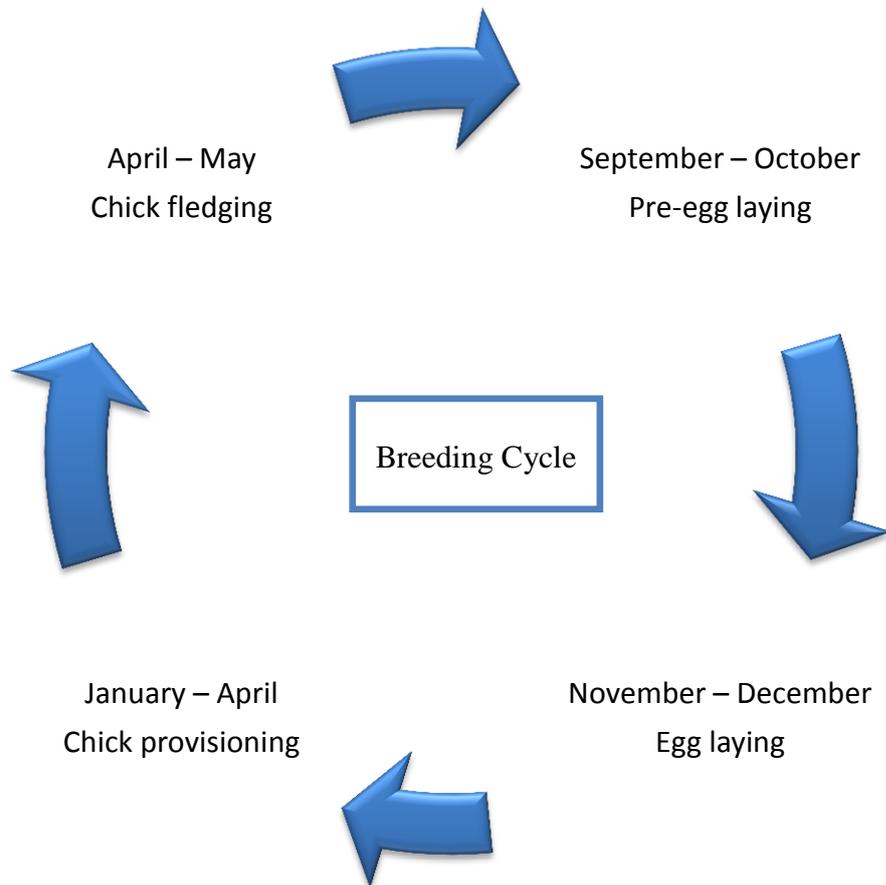


Figure 1.1 The annual breeding cycle of Gould's Petrel.

Stomach contents collected from Gould's Petrels suggest that in March, near the end of the chick rearing period, the species forage in coastal areas of the south-western Tasman Sea, possibly near Tasmania (McGee 2009). However, the validity of this suggestion is uncertain because chick stomach contents may contain the remains of food provided from many weeks of parental foraging. Overcoming this uncertainty requires information on the exact timing and direction of foraging movements, or the individual spatial and temporal patterns of habitat use, via the tracking of individual birds (Croxall et al. 2005, Shaffer et al. 2006). Data on the prey species of Gould's Petrels with data obtained via tracking will inform forecasting changes of movements as a result of climate change (Wormworth & Mallon 2014).

The primary breeding location of Gould's Petrel in Australia is CTI (32°41'19"S, 152°13'28"E; Figure 1.2) with a satellite colony, Boondelbah Island (32°42'S, 152°14'E). CTI is a 30-ha island, located 1.4 km offshore from Port Stephens, NSW and a nature reserve administered by the Office of Environment and Heritage. The island is aligned roughly north-south with the western side sloping steeply to 123 m above sea level. The eastern face falls precipitously into the sea. Several basaltic dykes dissect the toscanite bedrock from east to west, the two largest forming pronounced gullies containing extensive areas of rock scree. Rainforest dominated by Deciduous Fig (*Ficus superba*) and Cabbage Tree Palm (*Livistona australis*) covers much of the western slopes of the island and dense stands of Spiny-headed Mat-rush (*Lomandra longifolia*) dominate much of the remainder (Priddel & Carlile 2004).



Figure 1.2 Main breeding locations of Gould's Petrel.

1.4 THESIS GOAL AND AIMS

The Gould's Petrel is currently listed as endangered under the Commonwealth (Australian) Government's *Environment Protection and Biodiversity Conservation Act* 1999. In 2008, Gould's Petrel was downgraded to vulnerable under the State (NSW) *Threatened Species Conservation Act* 1995. This downgrading occurred because of improved breeding success at Gould's Petrel nest sites between 1989 and 2008 and the successful establishment of a second breeding population on nearby Boondelbah Island (Priddel & Carlile 2009). Rabbit grazing no longer poses a destructive threat to breeding habitat due to a successful rabbit eradication program (Priddel et al. 2000). Selective removal of Birdlime Trees (*Pisonia umbellifera*) and understorey re-growth has reduced the impact of sticky fruits immobilising chicks and adults, and avian predators have also been controlled (DEC 2006). Despite these on-island successes, the potential pressures to Gould's Petrels' survival when they are at sea are poorly known due to our limited knowledge of their at-sea movements.

The focus and priority of the conservation measures summarised above has been to increase successful breeding and minimise chick mortality at breeding grounds (Priddel & Carlile 2009). But efforts to protect seabirds are often confounded by the absence of information on their breeding biology and distribution at sea (Rayner et al. 2012). Information on changes in the spatial distribution and behaviour of birds at sea, and how these relate to the timing of key events in their annual breeding cycle, is essential for identifying and mitigating potential threats to the species at sea and for improving protection at the colony. The goal of this thesis is to investigate the breeding and foraging ecology of the endangered Gould's Petrel to increase and extend the knowledge base to inform the conservation and management of this threatened species. I will achieve this goal through the implementation of the following aims:

- Investigate foraging behaviour and variation in diet during the breeding season
- Investigate the potential impact of geolocators on breeding behaviour and compare different methods of monitoring chick provisioning rates;
- Investigate the incubation routines and associated body mass changes; and
- Provide recommendations for conservation of Gould's Petrel.

The outputs of this thesis will be of significant value in identifying and mitigating broader threats to Gould's Petrels and other small seabirds. The gathering of comprehensive data on prey species during the breeding season will also contribute to an ongoing international collaborative program aimed at characterising seabird 'hotspots'. This program enables greater understanding of the links between seabird communities and the wider food chain, and identifies the ecosystem-level processes under stress from overexploitation or global climate change.

1.5 STRUCTURE OF THE THESIS

This thesis is presented as a series of chapters that have been written in a format to facilitate publication in peer reviewed journals. Figure 1.2 illustrates the overall structure of the thesis.

Chapter 1 provides an introduction on the importance of animal movement data for conservation and the Gould's Petrel and seabirds generally.

Chapters 2 and 3 investigate and verify aspects of the tracking methodology implemented in later chapters. Chapter 2 has been accepted for publication in *Marine Ornithology*. I am the primary author of this manuscript. I conducted the analysis and wrote the chapter, Nicholas Carlile inspired the primary research questions, and David Priddel and Nicholas Carlile

assisted in the collection, interpretation and editing of data,. Chapter 3 is currently in review with *Wildlife Research*. I am the primary author of this manuscript. I conducted the statistical analysis, fieldwork and wrote the chapter. David Priddel inspired the primary research questions, and with Nicholas Carlile, assisted me in the field. John Merrick and members of my supervisory team assisted with interpretation of the data and editing of the manuscript.

Chapter 4 relates long-term incubation data and known pair histories with recent movement data to assess the seasonal routines and condition of adults. Chapter 4 is in review to submit to *Emu*. I am the primary author of this manuscript. I conducted the analysis and wrote the chapter. David Priddel and Nicholas Carlile provided me with data on adult body mass that was collected in 1996. John Merrick and members of my supervisory team assisted with interpretation of the data and editing of the manuscript.

Chapter 5 investigates foraging movements during the chick provisioning period. I conducted the analysis and wrote the chapter. I was assisted in the field by David Priddel and Nicholas Carlile. Ben Arthur at the University of Tasmania, Mark Miller at BirdLife International and Alana Grech assisted with model development. John Merrick and members of my supervisory team assisted with interpretation of the data and editing of the manuscript.

Chapter 6 summarises the key findings of this thesis and discusses the broader implications for conservation of this small threatened petrel.

In Appendix A, I include a manuscript on movements of Gould's Petrel during a non-breeding season (Priddel et al, in review). I contributed fieldwork data on Cabbage Tree Island collected during my PhD. Migration and behaviour during the non-breeding season is directly related to parent condition during the breeding season so I tracked birds during the non-breeding season of 2010 to study the influence of migration on breeding performance as

part of this PhD. Unfortunately, a technical malfunction meant that none of the tracking devices were operational.

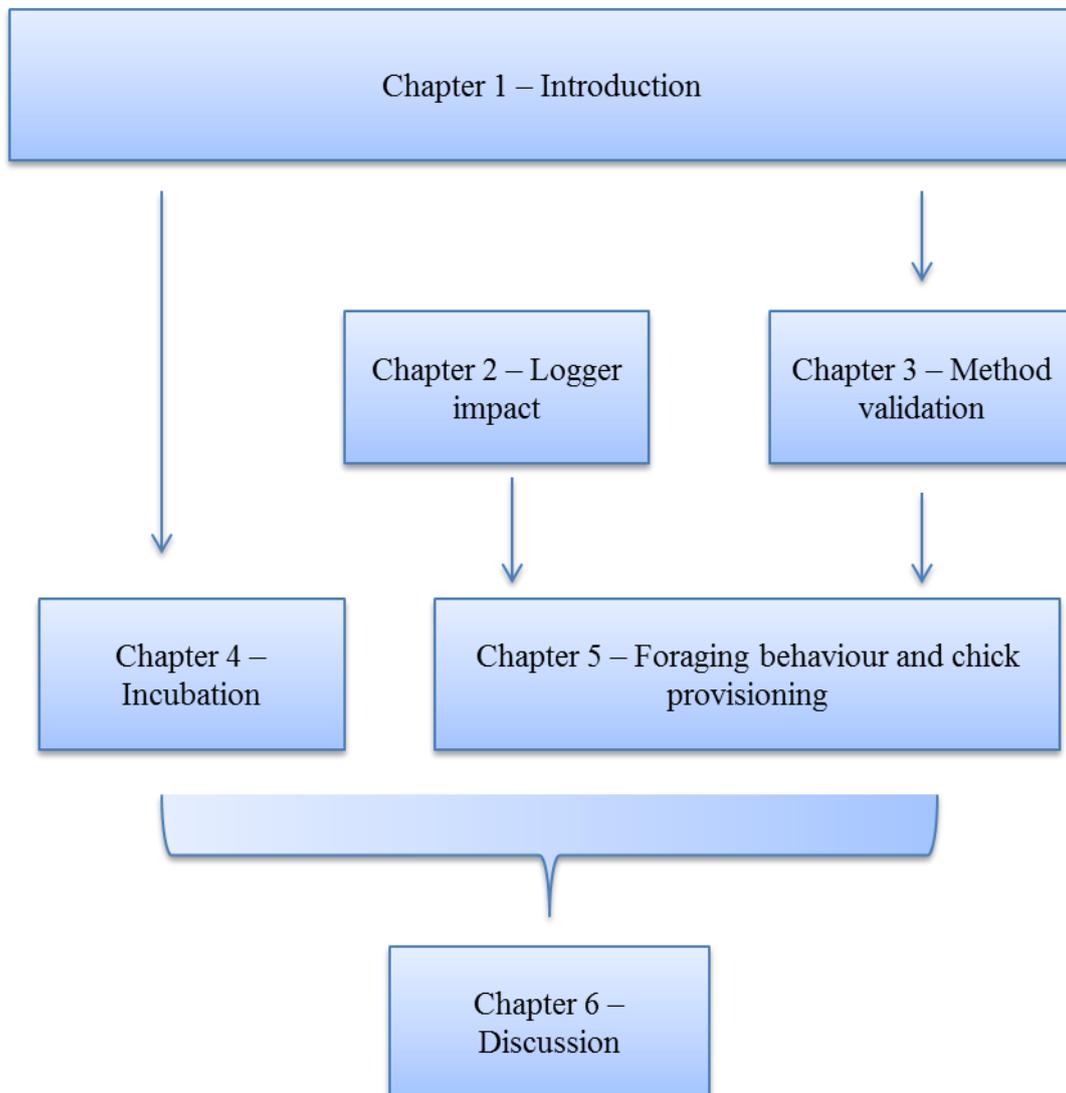


Figure 1.3 Summary of thesis structure and connections.

2 CHAPTER 2 - DO TRACKING TAGS IMPEDE BREEDING PERFORMANCE IN THE THREATENED GOULD'S PETREL *PTERODROMA LEUCOPTERA*?¹

2.1 ABSTRACT

Effects of tracking device deployment have been studied in large seabirds but less in small seabirds. Given the widespread use of tracking for distribution and foraging research, understanding whether attachment of such devices impedes breeding performance is critical. We examined the effects of both short- and long-term deployment of geolocators on Gould's Petrel (*Pterodroma leucoptera*) at Cabbage Tree Island (CTI), Australia, during the 2010–11 breeding season. We monitored breeding adults and their chicks over the 3 month period they carried geolocators. No significant effect on hatching success, fledging success or chick fledging mass was found. Body mass of adults carrying geolocators declined during the breeding season, but this was similar to birds without geolocators. No detectable negative impact was found for long-term (8–9 month) deployment during the non-breeding season on body mass or subsequent breeding performance. These findings suggest the use of small (1.5–2.0 g) geolocators does not inhibit foraging success and chick provisioning in Gould's Petrel. Similar verification in other small migratory seabirds fitted with geolocators is recommended.

¹ Kim, Y., Priddel, D., Carlile, N., Merrick, J.R. and Harcourt, R. 2014. Do tracking tags impede breeding performance in the threatened Gould's Petrel *Pterodroma leucoptera*? *Marine Ornithology* 42: 63-68. Submitted 21 September 2013, accepted 9 March 2014.

2.2 INTRODUCTION

Our understanding of the movements of wide-ranging marine predators has been revolutionised over the last three decades as a result of the development of tracking technologies (Croxall et al. 2005, Egevang et al. 2010). Progressive miniaturisation of devices has made it feasible to extend investigations from a few large species (e.g. albatrosses and giant petrels; (Rubenstein & Hobson 2004)) to many smaller species. Until recently, platform terminal transmitters (PTT) and global positioning systems (GPS) packages were relatively heavy for small birds (PTT >9 g and GPS >20 g; Burger and Shaffer 2008). Geolocators, also known as loggers, are comparatively small and lightweight (~2 g). They function by recording ambient light levels which, when integrated with an accurate clock, can be used to estimate longitude based on deriving local noon and comparing to GMT, and latitude based on determining day-length (Afanasyev 2004). However, unlike PTT or GPS, geolocators yield only one or two locations per day and so have usually been used for long-term deployments rather than short-term studies (Burger & Shaffer 2008). The accuracy of geolocators (ca. 200 km; (Phillips et al. 2004, Shaffer et al. 2005) precludes their application for studies involving species that travel over relatively short ranges.

Geolocators that log data must be retrieved from the animal to allow the download of information. They are effective tools for use with philopatric species in which there is a high degree of certainty of recapturing the study animals (Fiedler 2009). Attaching devices of any kind to flying birds is likely to affect their aerodynamics, and repeated capture to download data may induce capture and handling stress. These impositions may interfere with the animal's normal behaviour, leading to the collection of biased data (Carey 2009). A device mass of >3% of bird body mass is generally accepted as a critical point above which normal

behaviour is impaired (Phillips et al. 2003). However, some studies (e.g. (Wanless et al. 1988, Paredes et al. 2005, Ackerman et al. 2009, Adams et al. 2009) have found that even lighter devices (0.7–3.0% of body mass) have caused reduction in adult body mass, offspring attendance, provisioning rates and/or frequency of foraging trips. All of these studies were undertaken on relatively large birds, whereas few have investigated the effects of geolocators on small seabirds (Rayner 2007, Quillfeldt et al. 2012, Rayner et al. 2012). In addition, none of the aforementioned studies clearly demonstrated whether the adverse effects resulted from capture and handling, or whether the device reduced foraging efficiency (Carey 2009).

P. l. leucoptera (Gould's Petrel) is the smaller of two subspecies of the *Pterodroma leucoptera* species complex, (~205 g), and breed principally on Cabbage Tree Island (CTI) (32°41'20"S, 152°13'29"E), 1.4 km off Port Stephens, New South Wales, Australia. Although conservation issues for this subspecies at the nesting sites are well studied, little is known about its at-sea movements or foraging ranges (DEC 2006). Knowledge of movement patterns at sea is critical for developing management and conservation strategies (Priddel & Carlile 2009). The opportunity to obtain such information is now feasible because of the recent availability of small, lightweight geolocators. There is a need to identify risks of attaching such devices because of the uncertainty and limitations previously explained.

Although previous research had found that handling adult Gould's Petrel over a 7–10 day period during the incubation stage did not affect chick growth rates or survival (O'Dwyer et al. 2006a), there are four possible areas where negative effects might be important. First, long-term deployment of geolocators during the non-breeding season might have negative consequences on the birds' breeding success in the following year by influencing body condition before breeding. Second, the impost of carrying a geocator may affect foraging

performance, resulting in less frequent or smaller meals fed to chicks, thereby leading to a reduction in fledging success. Third, the additional stress from recapture and handling during and after the hatching period might also have adverse impacts on breeding performance. Finally, tag deployments could affect the rate of adults return to the colony, as a result of either tag-induced mortality or birds returning to a different location. The goal of this chapter is to investigate potential impacts of attaching a geolocator, with multiple capturing and handling, on the foraging behaviour of breeding adults of Gould's Petrels. I measured several breeding parameters, as foraging performance is directly related to breeding performance (Rayner et al. 2008). I also investigated whether changes in behaviour could be detected by comparing adult body mass and hatching success between adults with and without geolocators. I also compared the fledging body mass and fledging success of their chicks as body condition of parents correlated positively with the body condition of their chick at its peak mass.

2.3 MATERIALS AND METHODS

The study was carried out on CTI between March 2010 and April 2011. The principal breeding habitat of Gould's Petrel is concentrated within two steep gullies on the western side of the island (Priddel et al. 2006b). Since 1989, natural nests (marked by numbered tags) and artificial nest boxes have been surveyed annually to estimate population size, breeding success and reproductive output (Priddel & Carlile 2009). A nest box and entrance tunnel is illustrated in Figure 2.1; detailed description of the artificial nest boxes can be found in Priddel & Carlile (1995a).



Figure 2.1 A typical artificial nest box (left) used to trap adult birds at night. The gate on the entrance tunnel (top right and bottom) opens inward but not outward. Displacement of the stick (shown in the tunnel, top right) indicated the presence of an adult bird.

Gould's Petrels are sexually monomorphic (O'Dwyer et al. 2006c) and nocturnal on land, arriving after sunset and leaving before sunrise. Adults first return to CTI to breed from mid-to late September (DEC 2006). Egg laying commences in early November and, on average, 49 days are needed for incubation. As with all Procellariiformes, a single egg is laid; if lost, the egg is not replaced in the same season (Warham 1990). Following hatching, a parent broods the chick for 2–3 days; thereafter, it is fed infrequently by the parents until it fledges in April or early May (Priddel & Carlile 1995b).

The study was carried out in a sub-colony estimated to number approximately 1000 breeding pairs (Priddel et al. 2006b). Many of the adult birds are identifiable by a metal band inscribed with a unique number, and chicks are banded in March each year (Priddel et al. 2006b).

2.3.1 DEPLOYMENT DURING THE NON-BREEDING SEASON

During 22–25 March 2010, 42 geolocators were fitted to Gould’s Petrel adults taken from 35 nests (7 pairs, 28 single birds). Adults were captured while returning to the nest to feed their chick. Twenty MK14 (British Antarctic Survey; 1.5 g) and twenty two LAT2900 (Lotek; 1.9 g) geolocators were attached to the legs of adult birds using Darvic bands (Figure 2.2). Each MK14 (20 × 9 × 5.5 mm) was attached using a single cable tie and fast-drying cyanoacrylate adhesive (Supa glue; Figure 2.2 A). Each LAT2900 (20 × 8 × 6.7 mm) was attached using two cable ties as well as the adhesive (Figure 2.2 B). The resulting packages weighed 2.0 g (MK14) and 2.5 g (LAT2900), equivalent to 1.0%–1.3% of average body mass. Logger attachment was completed within 15 min of capture.

Geolocators were retrieved in the following breeding season, between 23 November and 27 December 2010, and the mass of birds recorded to the nearest gram with a 300 g Pesola spring balance. This sample group is hereafter referred to as NBLOGGER. Twenty additional nests were selected randomly and the adult occupants (hereafter referred to as NBCONTROL) were weighed at the same time as NBLOGGER to test for differences in mass as a means of assessing the impact of geolocators deployed throughout the non-breeding season.

The nests of both instrumented and non-instrumented birds (NBLOGGER and NBCONTROL, respectively) were inspected during 23–25 November and 13–15 December 2010 to determine whether laying had occurred and during 7–10 March 2011 to assess chick survival. Very few chicks die late in the nestling period (Priddel & Carlile 1997a), so advanced chicks present in March were assumed to fledge successfully.

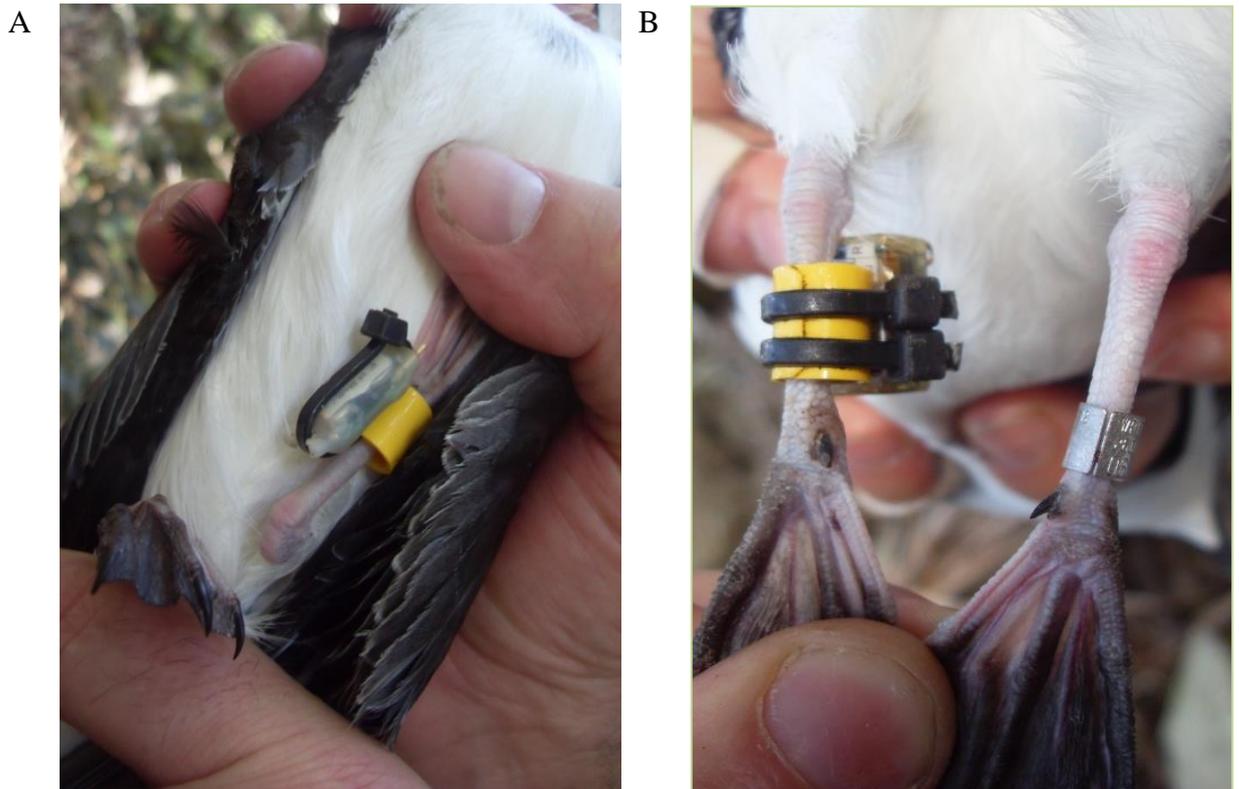


Figure 2.2 Attachment of two types of geolocators: (A) MK14 with a Darvic ring and single cable tie; (B) LAT2900 with a Darvic ring and two cable ties.

2.3.2 DEPLOYMENT DURING THE BREEDING SEASON

In late December 2010, I inspected all artificial nest boxes, except those housing birds used in the non-breeding study (NBLOGGER and NBCONTROL), to locate nests containing incubating adults. I then candled the eggs to assess whether they were viable. Twenty birds incubating viable eggs were selected for attachment of geolocators. If a selected bird changed incubation duties with its partner during the week-long sampling period, the second bird was also fitted with a geolocator. This sample group is hereafter referred to as **LOGGER**. Failed breeders leave the nesting grounds, so selecting viable eggs maximised the likelihood of the instrumented birds returning and thus increased the chance of retrieving the geolocators to

download data. Another 20 pairs from artificial nests boxes with viable eggs were captured and weighed in the same manner as LOGGER, but were not fitted with geolocators; these are hereafter referred to as NOLOGGER. A third group of 20 adult pairs, from natural nests containing viable eggs, were neither fitted with geolocators nor captured; these are hereafter referred to as CONTROL. The purpose of the CONTROL was to provide a measure of incubation success, fledging success, fledging mass and approximate meal size against which to compare LOGGER and NOLOGGER. Adults in CONTROL nests were not handled, but the chicks were.

Trapping adults as they returned to the nest to feed their chick was only practicable for birds that nested in boxes. So LOGGER and NOLOGGER nests were selected from among occupied nest boxes. A shortage of additional occupied nest boxes meant that the CONTROL sample had to be selected from natural nests.

During 2–10 January, 8–15 February, 5–9 March and 10–22 April 2011, two people continuously monitored all LOGGER and NOLOGGER nests between 2000 and 0300. Whenever an adult was intercepted, it was weighed, and birds with geolocators had data downloaded. All chicks from all three groups were weighed at approximately 1200 and 1800 daily, and approximate meal size was determined from overnight weight increases. As I was interested in relative differences between groups rather than actual meal size, I ignored the possibility of underestimating meal sizes due to metabolic processes and defecation. Decreases in overnight masses were ignored, even if I knew the nest had been visited by a parent, as occasionally parents will visit the nest without delivering food to the chick (Hamer & Hill 1993, Phillips & Hamer 2000).

LOGGER and NOLOGGER nest boxes were fitted with a removable one-way gate in the

entrance tunnel, which could flip inwards from outside, but could not open outwards in response to pressure from inside. The gates were fixed in place at 18:00 each day. A small stick was placed across the tunnel entrance, displacement of which indicated that a bird had entered the nest. From 20:00 nests were monitored and the visits of individual parents logged. When the stick had been dislodged, I opened the lid of the nest box and checked the contents. If an adult was present, the time was noted and approximately 30 min allowed for the adult to feed the chick. Adult birds were then captured and weighed, and data downloaded from those carrying geolocators. Adults were then returned to the nest box and the gate removed so they could leave. Monitoring ceased at 03:00, when all remaining gates were removed. Adults arriving after the gates were removed, either after one parent had been captured or after 03h00, were not detected.

2.4 DATA ANALYSES

I conducted statistical analyses using IBM SPSS statistic 21. All tests were two-tailed and considered significant at $P < 0.05$. Comparison of adult body mass between NBLOGGER and NBCONTROL was tested using an independent t -test. The Mann-Whitney U test was used for comparisons of adult body mass among LOGGER, NOLOGGER and CONTROL because the assumption of normality was violated and the data could not be transformed successfully. I compared hatching success, fledging success and breeding success between instrumented and non-instrumented birds using the chi-square test for goodness of fit. Kruskal-Wallis one-way analysis of variance by ranks was employed to compare fledging mass (due to small sample sizes) and mean meal size (due to non-normality).

2.5 RESULTS

2.5.1 EFFECTS OF DEPLOYMENT DURING THE NON-BREEDING SEASON

Forty of the forty two geolocators deployed during the non-breeding season were retrieved; thirty three tagged birds were weighed, seven intercepted by associates were not. At the beginning of the 2010–11 breeding season, the body mass of adults that had carried geolocators throughout the non-breeding season did not differ from that of non-instrumented birds (Table 2.1). A proportion of birds that carried geolocators failed to lay eggs (14%), whereas 5% of non-instrumented birds failed to lay, a difference that was not significant (Table 2.1). Hatch rates were 60% for instrumented birds and 42% for non-instrumented birds, and again not significant (Table 2.1). All chicks that hatched ($n = 26$, Table 2.1) fledged successfully.

Table 2.1 Effect of deployment of geolocators during the non-breeding season.

| Outcome | NBLOGGER | NBCONTROL | Test result | df | P |
|---|----------------------------------|----------------------------------|--------------------|-----------|----------|
| Adult body mass at the beginning of the breeding season, mean \pm SD, g | 209.2 \pm 20.4 ($n = 33$) | 213.2 \pm 17.2 ($n = 20$) | $t = 7.4$ | 51 | 0.46 |
| Egg-laying success, % (no./n) | 86 (30/35) | 95 (19/20) | $\chi^2 = 1.13$ | 1 | 0.29 |
| Hatching success, % (no./n) | 60 (18/30) | 42 (8/19) | $\chi^2 = 1.50$ | 1 | 0.22 |
| Fledging success, % (no./n) | 100 (18/18) | 100 (8/8) | | | |

2.5.2 EFFECTS OF DEPLOYMENT DURING THE BREEDING SEASON

No incubating adult fitted with a geocator abandoned its egg. Of the 60 eggs in study nests, 47 hatched (Table 2.2), and there was no difference in hatch rates among groups (LOGGER, NOLOGGER and CONTROL).

Fledging success was consistently high across all groups (Table 2.2). Of 15 chicks from the

LOGGER group, one was found dead in the nest; all others fledged successfully. The nest containing the dead chick continued to be monitored to retrieve the geolocators from the parents. I found that the nest was attended by at least three adults, and disputes over nest ownership are likely to have contributed to the death of the chick. Similarly, in the CONTROL group all chicks except one fledged. The failed chick disappeared from the nest without a trace six days after hatching, presumably due to predation. All 16 chicks from the NOLOGGER group fledged.

Breeding success (the proportion of eggs that produced fledglings) was 70–80% and was similar in all groups (Table 2.2). Fledging mass could be measured for only 11 chicks from LOGGER, 7 from NOLOGGER and 10 from CONTROL, because fledging commenced before the final sampling period. Fledgling mass was similar across all groups (Table 2.2)

The overnight increase in body mass was regarded as approximating meal size. Meal sizes were highly variable (range 1–88 g) and not significantly different between groups (Table 2.2).

Table 2.2 Effect of deployment of geolocators during the breeding season.

| Outcome | LOGGER | NOLOGGER | CONTROL | Test result | df | P |
|---------------------------------|------------------------------|-----------------------------|------------------------------|--------------------|-----------|----------|
| Hatching success, % | 75 (15/20) | 80 (16/20) | 80 (16/20) | $\chi^2 = 1.96$ | 2 | 0.91 |
| Fledging success, % | 93 (14/15) | 100 (16/16) | 94 (15/16) | $\chi^2 = 1.081$ | 2 | 0.58 |
| Breeding success, % | 70 (14/20) | 80 (16/20) | 75 (15/20) | $\chi^2 = 0.53$ | 2 | 0.77 |
| Fledging mass, mean \pm SD, g | 177.5 \pm 16.0 (n = 11) | 175.3 \pm 15.4 (n = 7) | 181.8 \pm 15.9 (n = 10) | $\chi^2 = 1.00$ | 2 | 0.61 |
| Meal size, mean \pm SD, g | 20.4 \pm 14.9 (n = 72) | 21.1 \pm 14.1 (n = 97) | 16.9 \pm 9.9 (n = 108) | $\chi^2 = 4.3$ | 2 | 0.12 |

Instrumented birds (LOGGER) lost mass between attachment (December 2010 to January 2011) and when next intercepted (February to April 2011) (Table 2.3; Kruskal-Wallis = 8.658, df = 3, P = 0.034, n = 68). However, body mass during February to April was no less

for tagged birds than for non-tagged birds (Table 2.3).

Table 2.3 Adult body mass change during the breeding season 2010–2011

| Group, mean \pm SD (n), g | | | | | | |
|-----------------------------|----|-----------------------|-----------------------|------------------------------|----------------|----------|
| Date record | of | LOGGER | NOLOGGER | Test result (Mann–Whitney U) | Standard error | <i>P</i> |
| Dec–Jan attachment | | 198.9 \pm 23.5 (15) | Not weighed | | | |
| Feb | | 179.2 \pm 11.9 (28) | 173.0 \pm 13.1 (17) | 163.5 | 42.6 | 0.08 |
| Mar | | 182.3 \pm 17.1 (19) | 180.7 \pm 22.2 (16) | 134.5 | 30.1 | 0.57 |
| April | | 176.2 \pm 24.3 (6) | 150.5 \pm 3.5 (2) | 0 | 3 | 0.71 |

2.6 DISCUSSION

Conservation programs for many petrels, including those in Australia, have focused on breeding success at nesting sites, but it is now recognised that data on movements at sea are also critical for elucidating habitat use, migratory corridors and time-activity patterns (Shaffer et al. 2006, González-Solís et al. 2007, Priddel & Carlile 2009, Croxall et al. 2012, Madeiros et al. 2012). This recognition, together with the development of small economical geolocators, has facilitated research into the movements and migration patterns of many species. However, it is essential to verify that deployment of geolocators does not adversely impact the birds targeted, either by changing behaviour or by reducing breeding productivity. Such impacts could affect the quality of the data collected and therefore mislead broader ecological interpretations that may have proven effective in improving the conservation status of seabird populations.

In this chapter, I did not detect any significant effect of geocator deployment on the breeding performance of Gould’s Petrels. While my findings were reassuring, sample sizes for some parameters (e.g. fledging success) were small, and significant effects may be discernible with larger samples. If the final sampling period was planned before fledging

commenced, the sample size of fledging success could be larger and differences in fledging dates could be used as an index of chick provisioning and included in this study. Adult body mass at the beginning of the season was used as an index of non-breeding ground conditions and the differential impact of loggers. This index might be impacted or biased by local food availability because adults of typical Procellariiformes spent time locally for about a month prior to egg-laying. If the information of how long adults used local resources before being weighed could be collected, this potential bias could be removed. Additionally, this study was carried out at a site where artificial nest boxes have been used for many years, which might provide more benign habitat and positively affect breeding success (Madeiros et al. 2012). All birds were released back into the tunnel of the nest box and immediately settled back onto the egg, and no nest was abandoned after geolocator deployment. However, the possibility of nest desertions in natural nests following the deployment of tracking devices has been suggested by other researchers (e.g. (Phillips et al. 2003)).

All deployments on Gould's Petrels during the breeding season involved birds that were nesting in boxes. Due to a shortage of occupied nest boxes in the study area, data from these birds were compared with those from birds nesting in natural nest sites. No differences were detected, and there is no evidence that this confounding factor affected the outcome of this study.

Although I found no significant impacts of geolocator attachment on breeding performance, a comparative trip duration analysis may be a more sensitive indicator of the costs of carrying devices. Typically, foraging trips are prolonged following PTT attachments (~67% of studies reviewed in Phillips et al. 2003). For example, tagged Common Murres (*Uria aalge*) made fewer but longer trips away from the nest and provisioned their chicks significantly less

frequently than their non-tagged partner (Wanless et al. 1988). Although I determined that there were no differences in approximate meal size and that nearly all chicks developed well enough to fledge, it is plausible that their parents expended more energy to perform similar provisioning effort compared with other non-tagged or non-handled birds. Comparatively, Carey (2011) questioned whether tagged adults could provision themselves, as well as their offspring, adequately.

Despite widespread acceptance of the “3% rule” suggested by Phillips et al. (2003), Barron et al. (2010) found little evidence that negative effects increased as devices became proportionally heavier. Rather, the method of device attachment was deemed to be more important. Harnesses and collars had more negative effects than the leg-band attachment used here. However, I found using glue can cause skin abrasion if not carefully applied (Figure 2.3). Excess adhesive can stick the Darvic ring to the bird’s leg, causing superficial damage, so care must be taken when using this method. The time for glue to dry also varies with temperature, and this can affect handling time (Adams et al. 2009). I altered my attachment protocol and ceased using glue in subsequent deployments, replacing the Darvic band with Velcro and Tesa tape. However, this modification increased the mass of the attachment, causing abrasions at the base of the leg near the joint on long-term deployments (longer than 4 months). To avoid or minimise such negative impacts during long-term logger deployments, the mass of the equipment, frequency of handling and length of deployment should all be minimised, with the geolocators removed from the birds at the earliest possible time.

Data collected using new technologies are invaluable for understanding where seabirds forage and which parts of the ocean form critical habitat in their life cycle. However, to optimise the insights from such research, it is essential that it is done in a manner that does not interfere

with breeding success or foraging habits of the study animals. I strongly recommend conducting similar experimental studies of logger impacts on any other species proposed for large-scale deployments. Relatively smaller procellariiform seabirds, such as the Fork-tailed Storm-petrel (*Oceanodroma furcata*) (Boersma et al. 1980), Tristram's Storm-petrel (*O. tristrami*) (Marks & Leasure 1992) and Leach's Storm-petrel (*O. leucorhoa*) (Blackmer et al. 2004), show negative impacts from short-term handling. Therefore, when tracking devices are small enough to be deployed on these species, it is recommended that researchers investigate possible attachment and handling effects before large-scale movement studies to ensure minimal detrimental impacts. The documentation of any disturbance effects caused by scientific research may be crucial for designing future research or conservation programs (Carey 2009).



Figure 2.3 Abrasion caused by accidental leakage of glue on to the leg resulting in the Darvic band adhering to the leg.

3 CHAPTER 3 - TESTING THE RELIABILITY OF DIRECT AND INDIRECT TECHNIQUES TO MONITOR NEST ATTENDANCE IN SMALL SEABIRDS²

3.1 ABSTRACT

Determining nest attendance patterns of seabirds can give important insights into foraging ecology and energetic trade-offs. Previous studies have often combined techniques to monitor nest attendance but there is a need to determine the reliability of measurements made by each method. This study aims to investigate reliability and practicality of four different techniques (trapping adults, measuring mass change in chicks, examining images from infrared cameras and analysing temperature data from geolocators) to calculate nest attendance rates of Gould's Petrel (*Pterodroma leucoptera*) during the breeding season. Data obtained using each method were analysed separately to estimate independently the rate of nest attendance. Although data sets varied in timing and duration, the calculated frequencies of nest attendance were similar. Although Krippendorff's alpha value was low, Cohen's kappa test validated that each method has at least moderate agreement with other methods. Each technique has practical limitations, however, I suggest strategies to alleviate impacts or prevent problems. The least disturbance to adult birds was from the use of infrared cameras. Temperature loggers in geolocators can be used to determine nest visits, enabling resolution of short-term foraging and provisioning behaviour. This approach of integrating data sets is recommended for studies of other small seabirds that, due to their mass, have weight limitations on the devices they can carry.

² Kim, Y., Priddel, D., Merrick, J.R., Carlile, N. and Harcourt, R. *in review*. Testing the reliability of direct and indirect techniques to monitor nest attendance in small seabirds. Wildlife Research

3.2 INTRODUCTION

Life history theory predicts that decisions about the allocation of reproductive effort may be affected by the individual's current body condition (Sterns 1992 in Numata et al. 2000). For example, immediate reproductive effort of an individual in poor condition may be curtailed in order to maximise its lifetime productivity (Dearborn 2001). Among species with biparental care, decisions may also be based on the level of effort put forth by one's mate (Davies & Houston 1986) and, generally, nest attendance patterns during the breeding season reflect the way time is allocated between the conflicting demands of breeding and foraging (Numata et al. 2000). Therefore monitoring avian nesting behaviour provides a temporal framework for ethological, physiological and ecological investigations (Cooper & Afton 1981).

By measuring the frequency of nest attendance, the duration of foraging trips can be calculated, which can then indicate foraging behaviour during breeding. Aside from contributing to essential knowledge on breeding biology, information about nest attendance patterns can assist in scheduling research activities. For example, knowing the duration of incubation shifts or provisioning patterns makes capturing of targeted birds easier, minimising or avoiding long observer waiting times. The advantages of efficient field strategies are clear, in terms of time, cost and the use of non-invasive methods.

Many methods have been used to reveal nest attendance of seabirds, during both the incubation and chick rearing periods (Simons 1981, Ricklefs 1984, Ricklefs et al. 1985, Weimerskirch et al. 2001, Hoover et al. 2004, Zangmeister et al. 2009, Shoji & Gaston 2010). Techniques include marking birds and daily inspection of burrows, knock-down tags, photographic or video cameras, event recorders, passive integrated transponder (PIT) tags, radio telemetry, logging temperature, and measuring changes in chick mass. Previous studies

have often combined two or more of these techniques in order to reduce biases of individual methods, however there remains a need to determine the reliability of each method.

The foraging behaviour of Gould's Petrel (*Pterodroma leucoptera*), determined through the use of geolocators was, until recently, unknown (Priddel et al. in press). Geolocators record light level and this can be used to calculate latitudinal and longitudinal fixes when articulated with accurate time after data are retrieved (Afanasyev 2004). The limitation of using geolocators is precision; only one or two locations per day can be generated with the mean accuracy \pm SD of 169 ± 104 km (Phillips et al. 2004). Although still useful as a means of identifying core foraging locations during the breeding season, the high error range of locality data creates difficulty in determining whether birds are foraging close to the breeding site or visiting the nest. A few previous studies of other seabirds (Phillips et al. 2006, Rayner et al. 2008) predicted the instrumented bird was in the nest when continuous low light levels corresponded with daylight hours. This does not apply for Gould's Petrel as provisioning visits are only at night for a short time. We attempted to overcome this by assessing temperature differences when the adult was inside versus outside the nest. Zangmeister et al. (2009) found the mean difference between temperatures in the nest and in the entrance tunnel was $4.5 \pm 1.9^\circ\text{C}$ and concluded that sustained differences greater than 2.0°C would indicate the presence of an adult in the nest.

This chapter aims to investigate reliability and practicality of four different techniques (trapping adults, measuring mass change in chicks, examining images from infrared cameras and analysing temperature data from geolocators) to calculate nest attendance rates of adult Gould's Petrel during the 2011–12 breeding season. It is of particular interest to examine the feasibility of using temperature data from geolocators to monitor nest attendance, which can

be useful for further analyses of tracking data during the breeding season. In so doing, I aim to provide more efficient methods to investigate nest attendance patterns in other seabird species.

3.3 MATERIALS AND METHODS

Gould's Petrel breed during the Australian summer to autumn months, showing the typical procellariiform pattern of a single-egg clutch with a long incubation period (mean 49 days, Kim et al. in press), slow chick development, and protracted fledging period (mean 90 days, O'Dwyer 2004). They nest deep underground in cavities among rock scree, but readily take to nesting in artificial nest boxes. Laying commences in mid-November. Chicks hatch from early January and fledge late March to May. Parents seem to brood for 1–2 days, thereafter the parents return to feed the chick at night.

3.3.1 STUDY SITE

The study was carried out at Cabbage Tree Island (CTI) (32°41'20'S, 152°13'29'E), 1.4 km off the coast of Port Stephens, NSW, from December 2011 to December 2012 (Figure 1.2). The main nesting sites on CTI are concentrated in two gullies characterised by steep rock-scrub slopes with a canopy of Cabbage Tree Palm (*Livistona australis*) on the western side of the island (Fullagar 1976). The study was conducted in the south gully using 10 artificial nest boxes containing breeding pairs that were each individually marked with a unique numbered leg band. The boxes are described in Priddel & Carlile (1995).

3.3.2 OVERNIGHT MASS CHANGE OF CHICKS

Sampling was conducted 5–14 and 19–21 January, 3–18 February, 24 March – 7 April and 25–27 April 2013 during the chick provisioning period. Chick mass (nearest gram) was measured with a 300 g or 500 g Pesola spring balance around 1200 and 1800 daily to record overnight mass increases arising from provisioning visits by the parents. I defined a ‘visit’ when the mass increased and ‘no visit’ when there was no change or a decrease in mass.

3.3.3 TRAPPING

One-way gates, made from a piece of Plexiglas, were attached to the inside of the tunnel entrance of the 10 nest boxes. Gates were activated in late afternoon, and monitored from approximately 2000 to 0300. To minimise disturbance, I placed a small stick across the tunnel entrance. Displacement of the stick indicated that a parent might have entered and the lid of the nest box was then opened and the box checked for the presence of the adult. Once the presence of an adult was confirmed, the time was noted and a further 30 minutes allowed for feeding unless the adult was trying to leave. After the band number of the bird was recorded, the individual was returned to the nest box and the gate removed so that it could leave anytime. A ‘visit’ was recorded when a bird was trapped and ‘no visit’ when no bird was trapped.

3.3.4 CAMERA OBSERVATIONS

A HC500 HyperFire camera (Reconyx®, Wisconsin) was placed 1–3 m from the entrance of each of the 10 nest boxes from 12 December 2011 until chicks fledged (around the end of April 2012). All cameras except one were positioned to monitor parental visits from mid-incubation onward. As one egg failed, the camera was moved to another nest that already had

a 28-day-old chick. Figure 3.1 shows an example of the images from the cameras. Camera image data include records of time, date and ambient air temperature. To distinguish each parent, they were colour banded with a single plastic ring on the leg with the geolocator (see below) and two on the other. A ‘visit’ was recorded when photos showed any birds with a colour ring or a geolocator. If images of an adult did not show either geolocators or rings, I assumed this particular bird did not belong to the nest, and ‘no visit’ was recorded.

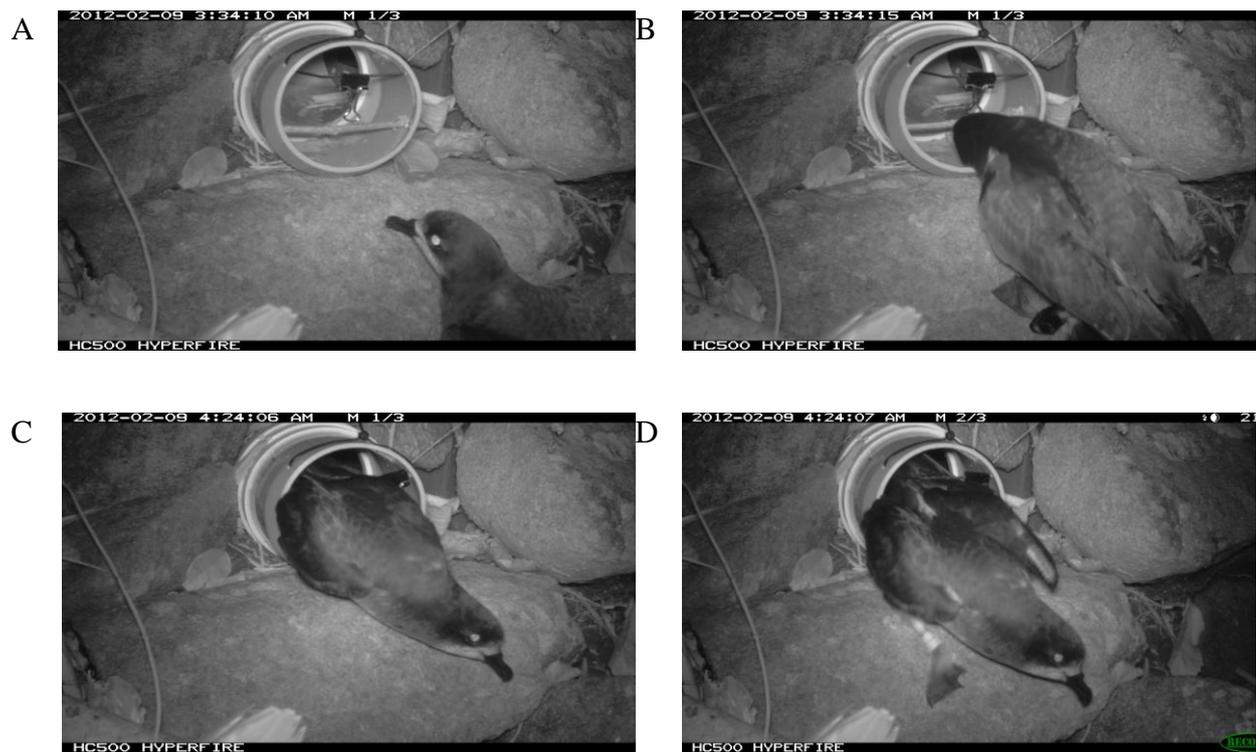


Figure 3.1 Images from an infrared camera. A: first appearance; B: The geolocator on the left leg confirms that the bird belongs to the nest; C: After 50 min, the bird comes out from the nest; D: two rings on the right legs confirm that the bird is a female.

3.3.5 TEMPERATURE DATA FROM GEOLOCATORS

Twenty geolocators (Star-Oddi®, Gardabaer, Iceland) were programmed to log light level and temperature every seven minutes. They were deployed on the 10 breeding pairs from 6 January 2012, using the attachment method described by Kim et al. (in press). Logger retrieval started on 25 March 2012 and, by 28 December 2012, 16 loggers had been recovered. One unit failed and seven units stopped logging earlier than expected (see results).

I selected temperature data from the loggers of instrumented adults that were known to be in the nest (i.e., trapped). The mean temperature in the nest was $28.5 \pm 0.6^\circ\text{C}$, however, the range varied from 18.0 to 34.8°C . When an adult entered the nest, the temperature increased $3.3 \pm 0.2^\circ\text{C}$. Upon leaving the nest, the temperature decreased $3.3 \pm 0.2^\circ\text{C}$. Therefore, I assumed a ‘visit’ occurred if either (1) more than four series of temperature readings were above 25.6°C (the mean minus one SD) at night (i.e., when light level of geolocators was lowest), or (2) a series of temperature readings equal or above 25.6°C was recorded with sustained differences greater than $\pm 3^\circ\text{C}$ before and after the series. Otherwise the status was scored as ‘no visit’.

3.3.6 STATISTICAL ANALYSES

All statistical analyses were performed using IBM SPSS statistic 21. All means are presented mean \pm SE. To assess the reliability of the four different methods, Krippendorff’s alpha (Further: KALPHA) was computed by the KALPHA macro (Hayes & Krippendorff 2007). KALPHA is a reliability estimate for judgements made at any level of measurement, any number of observers (in this chapter observers refers methods), and with missing data. However, if there is a method performing poorly, KALPHA can be misleading. Therefore I

calculated Cohen's Kappa pairwise to find out differences between pairs of methods. The Kappa statistic is a simple and effective evaluating agreement on a nominal scale (Cohen 1960). Reliability here is defined as the extent of agreement between judgements made by the different methods. The judgement here is nominal 'visit' or 'no visit'. For this study, according to (Manel et al. 2001), values of 0.0–0.4 are considered to indicate slight to fair model performance, values of 0.4–0.6 moderate, 0.6–0.8 substantial and 0.8–1.0 almost perfect. After confirming the reliability of methods, the number of true-positives, true-negatives, false-positives and false-negatives for each method were tabulated. Although I confirmed that camera monitoring performed best (see Results), there is no 'gold standard'. As a result, I considered true-positives and true-negatives when one of the three methods scored as 'visit' and 'no visit', respectively. When the indication of each method was not the same with one of the other methods it was considered as a false-positive or false-negative.

3.4 RESULTS

3.4.1 OVERNIGHT MASS CHANGE OF CHICKS

Overnight mass changes were measured during 29.5% of the days from hatching to fledging in the 10 nests. Chicks with an overnight increase in mass indicated a parental visit (44.1% of records) whereas no increase indicated no parental visit (55.9%). The mean mass increase overnight was 15.0 ± 0.9 g (range 1–60 g, $n = 121$) and the mean mass decrease was -5.6 ± 0.3 g (range -15–0 g, $n = 153$).

3.4.2 TRAPPING

The trapping period covered 31.5% of the total chick provisioning period of 92.7 ± 1.0 days (Table 3.1). Both parents were trapped on 0.3% of nights. On 26.7% of nights one parent was

trapped and the band number identified. Due to birds escaping before identification, 3.8% of visitors could not be identified. Overall, the attendance rate calculated from trapping data was 30.8%, with 69.2% of nights recording no visit.

3.4.3 CAMERA OBSERVATIONS

As mentioned above, one camera was set 28 days after hatching. The view of another nest's entrance was obscured by a fallen palm frond making it impossible to identify the visiting adults as belonging to the nest for a period of 17 days in March. Alignment of one camera was altered (perhaps by falling litter) and it was difficult to identify the visiting birds for about a month. However, overall the cameras were able to monitor 94.3% of the total chick provisioning period in the 10 nests. More images were captured when birds left the nests than when they entered (541 *cf.* 411), and 296 images (23.7%) did not clearly show the movements of individual adults (Table 3.2). After analysing the photographic images, I discovered that both parents visited nests on 3.8% of the monitored days. During 26.9% of the monitored days one of the parents visiting was identified by the rings, but on 11.5% of days it was not possible to determine which of the parents visited as the rings did not show. The overall attendance rate was calculated as 42.1% using the camera images (Table 3.1).

Table 3.1 Nest attendance rates calculated by different methods

| Methods (sum of total number of night used) | Mass change (274) | Trapping (292) | Photo (875) | Temperature (724) | Combined data accepting the case of temperature false-positive | Combined data ignoring the case of temperature false-positives |
|--|--------------------------|-----------------------|--------------------|-----------------------------------|---|---|
| One bird with identification (%) | n/a | 78 (26.7) | 235 (26.9) | 297 (41.0) | 395 (44.3) | 358 (40.3) |
| Double feeding (%) | n/a | 1 (0.3) | 33 (3.8) | 20 (2.8) | 57 (42.6) | 36 (38.6) |
| No identification (%) | 121 (44.1) | 11 (3.8) | 101 (11.5) | n/a | 16 (1.7) | 16 (1.7) |
| Attendance rate (%) | 121 (44.1) | 90 (30.8) | 369 (42.1) | 317 (43.8) | 468 (50.4) | 410 (44.2) |
| Coverage from hatching to fledging (%) | 29.5 | 31.5 | 94.3 | 1 logger: 78.0 2 loggers: 33.6 | | |

Table 3.2 Movements identified in infrared camera images

| Nest | Frequency (%) of movement | | | Total movements |
|-------|---------------------------|------------|------------|-----------------|
| | Outward | Uncertain | Inward | |
| G063 | 52 (44.1) | 31 (26.3) | 35 (29.7) | 118 |
| O013 | 105 (46.9) | 32 (14.3) | 87 (38.8) | 224 |
| O015 | 56 (44.4) | 30 (23.8) | 40 (31.7) | 126 |
| O016 | 77 (44.3) | 40 (23.0) | 57 (32.8) | 174 |
| O019 | 38 (43.2) | 24(27.3) | 26 (29.5) | 88 |
| O037 | 31 (26.1) | 56 (47.1) | 32 (26.9) | 119 |
| O038 | 53 (53.0) | 10 (10.0) | 37 (37.0) | 100 |
| O092 | 42 (38.2) | 38 (34.5) | 30 (27.3) | 110 |
| R168 | 63 (51.2) | 7 (5.7) | 53 (43.1) | 123 |
| Total | 541 (43.3) | 296 (23.7) | 411 (32.9) | 1248 |

3.4.4 TEMPERATURE DATA FROM GEOLOCATORS

These data were less extensive for three reasons: attachment of some of the geolocators was post-hatching; four geolocators could not be retrieved; and seven units unexpectedly stopped logging temperature. During the total chick provisioning period, temperature from both members of a pair could be logged 33.6% of the time, and one parent only for 44.4% of the time. In total, 78.0% of the time at least one logger could be used to calculate attendance rate, but for 22.0% of the time neither of the parent loggers were available (Table 3.1). A total of 317 visits were determined on the basis of temperature differentials, equivalent to a visitation rate of 43.8% (Table 3.1).

3.4.5 AGREEMENT BETWEEN METHODS

Inter-observer variability on parental visits was confirmed by a KALPHA reliability coefficient of 0.557, 95% CI: 0.388–0.714 (Units 751, Observers 4, Pairs 1924). Usually the low alpha value is caused when one or more methods are performing poorly. So I calculated the proportion of agreement between methods and used Kappa test pairwise (Table 3.3). The

proportion of agreement between temperature logging and trapping was high (92.3%), whereas the agreement between temperature logging and other methods was relatively low (~ 74%). Although KALPHA values were low for each individual method, the results of each method were correlated with that of others at least at the moderate agreement level. According to the Kappa test result, camera images with mass change or trapping have substantial agreement; this was expected due to the good performance of cameras in detecting parental visits. As mass change or trapping methods were only applied for limited times, those data were combined with camera data. The combined data and temperature data resulted in an agreement of 75.4% with a Kappa measurement, $k = 0.505$ (95% CI: 0.441–0.569, $Z = 13.415$, $p < 0.001$) and KALPHA of 0.504 (95% CI: 0.336–0.678, units 702, Observers 2, Pairs 702).

Table 3.3 Summary of KALPHA and Kappa test results

| Method 1 | Method 2 | The proportion of observed agreement | KALPHA | Kappa | Agreement | 95% CI | Z | Sig |
|----------|-------------|--------------------------------------|--------|-------|-------------|---------------|--------|-------|
| Mass | Trapping | 81.9 | 0.630 | 0.530 | Moderate | 0.532 - 0.744 | 9.259 | 0.000 |
| Mass | Camera | 89.9 | 0.774 | 0.799 | Substantial | 0.709 - 0.879 | 11.278 | 0.000 |
| Mass | Temperature | 72.9 | 0.467 | 0.459 | Moderate | 0.321 - 0.577 | 6.470 | 0.000 |
| Trapping | Camera | 82.2 | 0.663 | 0.636 | Substantial | 0.530 - 0.736 | 9.532 | 0.000 |
| Trapping | Temperature | 92.3 | 0.430 | 0.461 | Moderate | 0.323 - 0.587 | 6.579 | 0.000 |
| Camera | Temperature | 74.9 | 0.509 | 0.494 | Moderate | 0.363 - 0.621 | 6.985 | 0.000 |
| Combined | Temperature | 75.4 | 0.504 | 0.506 | Moderate | 0.441 - 0.569 | 13.415 | 0.000 |

The numbers of true-positives, true-negatives, false-positives and false-negatives for each method are tabulated in Table 3.4. Overall, chick mass change achieved high true-positives and high true-negatives, 39.8% and 52.9%, respectively. Reasons for the 2.9% of false-

negatives with chick mass might include small meal size or fast metabolism of the chick. Alternatively it may be due to measurement error; i.e., not recording an increase in mass after a parental visit. For false-negatives, it is possible that the camera was not functioning well, but considering the high performance rate of cameras (99.1%), it is more likely due to measuring mistakes. In summary, 92.7% of mass change data matched with other types of data in determining parental visits.

Table 3.4 Judgment results for each method compared with other methods (Percentages are in brackets).

| Methods | True-positives | False-positives | True-negatives | False-negatives |
|--------------------|-----------------------|------------------------|-----------------------|------------------------|
| Mass | 109 (39.8) | 12 (4.4) | 145 (52.9) | 8 (2.9) |
| Trapping | 90 (30.8) | 0 | 168 (57.5) | 34 (11.6) |
| Camera | 90 (30.8) | 0 | 498 (56.9) | 8 (0.9) |
| Temperature | 90 (30.8) | 68 (6.8) | 627 (62.9) | 41 (4.1) |

Trapping was also a relatively effective method with 88.4% of correct decisions. Overall, only 11.6% of parent visits were missed. This was the highest proportion of false-negatives of any method and was because I finished sampling around 0200. Extending the working hours could reduce the number of false-negatives.

Camera images had the highest accuracy among all methods, 99.1%. In only 0.9% (9 cases) did the night camera not capture images although a bird was trapped. On one night, three cameras did not function as they were inadvertently not activated. There were five other instances of malfunction, all on different nights, and causes remain unknown.

Temperature loggers had 89.1% accuracy. On 4.1% of nights the temperature logger was not able to show the visit although other methods did. Also temperature data gave false-positives on 6.8% of the nights, when no other method showed visits. Although there is a possibility of camera failure, as emphasised already, camera performance was very reliable; the false positives are more likely to be due to high ambient temperatures on warm summer nights.

If all data are combined, including cases when only temperature data shows a visit, the attendance rate becomes 50.4%. However, based on the high accuracy of camera images and excluding those temperature only cases, the attendance rate becomes 44.2%, which is similar to other methods (Table 3.1).

3.5 DISCUSSION

Although data sets differed in duration, all the techniques used in this chapter showed moderate agreement in nest attendance. The overall frequencies, calculated from my discontinuous data collection, suggest a visit every 1–3 days with 44.2% attendance rate, which, in other seabirds, is consistent with many short foraging trips to facilitate frequent provisioning of the chick (Chaurand & Weimerskirch 1994b).

3.5.1 OVERNIGHT MASS CHANGE OF CHICKS

Studies of foraging ecology during the breeding season usually involve measuring weight variation of the chick, typically with direct observations of adult provisioning. Overnight mass increase can indicate a parental visit and this method is convenient as it does not require the researcher visiting nests at night; however, as the data in this chapter show, these increases vary widely and a parental visit may not always be detected if a small meal is delivered and the chick loses mass rapidly due to the metabolic cost of digestion (Warham 1990). Other disadvantages are that visit times cannot be determined, and the identity of the visitor cannot be established. There is utility however, as my results using this method are consistent with the visit frequencies estimated by other methods.

3.5.2 TRAPPING

Direct observation at night with trapping is still widely used by many researchers, although deploying observers for extensive periods is both costly and laborious. As with my study, the collection of this type of data often cannot be continuous over a whole season (Warham 1990). There is also a possibility of disturbance to natural behaviour of both target and non-target species around the nesting site (Carey 2009) particularly by lights that are necessary to work at night (Rodriguez & Rodriguez 2009). Distinguishing individuals of the pair by marking the plumage around the head or neck could lessen the amount of handling, thereby reducing the level of disturbance. Stock marking sprays have been used successfully, however, periodic re-marking is usually required as the dyes fade with frequent diving.

3.5.3 CAMERA OBSERVATIONS

Using cameras has become common in wildlife research as they are relatively inexpensive and usually non-invasive (Williams & Wood 2002, Hoover et al. 2004, Locke et al. 2005, Pierce & Pobprasert 2007), but there are limitations. Humidity caused condensation on lenses and the resulting blurred images made it difficult to identify the bird. Adequate initial testing to position cameras at the right distance and angle is required and regular checks of both the camera and battery levels are also required. The use of modern high-capacity memory cards can eliminate data storage constraints, but limited battery life may necessitate frequent servicing visits. Typically, either infrared cameras or motion-sensor cameras are employed for wildlife research. As infrared cameras are triggered by heat intensity, they may not function effectively on birds insulated by feathers, particularly when individuals present their tails to the camera. This was shown in my results where more photos were taken when birds were coming out of the nest. To maximise the potential for detecting a visiting bird, it is

recommended that the camera be set up facing the side of the nest entrance or perhaps where the bird lands. Motion-sensor cameras are only successful if there is no vegetation in the field of view that is likely to move in the wind and cause false triggers.

In my study, the camera record was the most extensive observation method, covering almost the entire provisioning period, and visitation rates were consistent with those calculated from other methods. Photographic images also provided additional data such as exact timing and duration of visits as well as the identity of the visiting parent. Instances where the identity of the parent was uncertain could be reduced by marking the head or neck of one individual of the pair.

3.5.4 TEMPERATURE DATA FROM GEOLOCATORS

Miniaturisation now enables deployment of various tracking devices on small seabirds but weight limits still restrict tracking of small birds like Gould's Petrel to geolocators (Guilford et al. 2009). Although widely used to ascertain at-sea distribution of small petrels, deployment of geolocators is typically for long-term studies of migration and movements during the non-breeding season (Fiedler 2009, Harris et al. 2009, Quillfeldt et al. 2013). While the locality error range is high, some geolocators incorporate a temperature sensor that is used to refine location data, and I noted temperature differentials apparently associated with nest visits. If reliable, the use of temperature data from geolocators could replace the use of small data loggers in the nests or temperature-sensing probes or thermistors inside artificial eggs to investigate attendance patterns (Hoover et al. 2004). While my results showed that the increase/decrease of 3°C is a useful indicator, the absolute differential has to be treated with some caution as there was a relatively high rate of false-positives (6.8%). Combining cameras with geolocators would give the most comprehensive data about nest attendance and is

recommended. Alternatively, recently a number of studies have used PIT tags with other types of tracking devices (Weimerskirch et al. 2001, Welcker et al. 2009, Zangmeister et al. 2009). While, as Zangmeister et al. (2009) pointed out, PIT tags are less invasive due to their small size, PIT readers are costly and multiple units for remote monitoring can still be prohibitively expensive.

Guilford et al. (2012) points out that researching threatened species can be problematic because of their rarity and their sensitivity to disturbance. Employing less invasive methods is very important both for improving animal ethics and for ensuring that data obtained are not biased. Although the effect of handling and using geolocators on Gould's Petrel is apparently not large enough to cause negative effects on breeding birds (O'Dwyer et al. 2006a; Kim et al. in press), similar disturbance to other seabird species has caused reduction in adult body mass, changes in offspring attendance, lowering of provisioning rates and alteration of the frequency of foraging trips ((Wanless et al. 1988, Paredes et al. 2005, Ackerman et al. 2009, Adams et al. 2009). At worst, some species, such as the Fork-tailed Storm-Petrel (*Oceanodroma furcata*), are particularly prone to disturbance and will abandon the nest when handled or stressed (Boersma & Wheelwright 1979).

In this chapter, I have demonstrated successfully the low impact use of geolocators, fitted with temperature loggers, as a method that can be used to indirectly monitor the parental visiting pattern of threatened Gould's Petrel. Other studies (Granadeiro et al. 2009, Guilford et al. 2012) have used geolocators combined with saltwater immersion to determine whether the study bird visited the colony or remained at-sea by looking at the daily immersion profile (i.e., a dry period exceeding 5 hrs indicated a visit to the colony). Further research to investigate the reliability of this method on Gould's Petrel and other species is necessary.

4 CHAPTER 4 - INCUBATION ROUTINE AND ASSOCIATED CHANGES IN BODY MASS OF GOULD'S PETREL *PTERODROMA LEUCOPTERA*³

4.1 ABSTRACT

Procellariiformes have prolonged incubation shifts with breeding birds enduring long periods of fasting and significant reductions in body mass. These changes can be physically demanding and parents must balance their own energy requirements with those of their young. The incubation routine and associated changes in body mass of breeding Gould's Petrel (*Pterodroma leucoptera*) were studied to explore the relationships between body mass, incubation shift duration and nest desertion. The incubation routine of Gould's Petrel was similar to other Procellariiformes, although shift length was particularly long for a bird of this size. Unsuccessful hatchings were due to egg damage or nest desertion. Temporary egg abandonment was observed in successful as well as in failed breeders. Nest desertions generally occurred before the normal duration of the incubation shift rather than after excessively long shifts caused by the late return of the partner. I conclude that incubation success was limited by the condition of birds at the start of the shift and their tenacity to remain until relieved by their partner.

³ Kim, Y., Priddel, D. and Carlile, N. *In prep.* Incubation routine and associated changes in body mass of Gould's Petrel *Pterodroma leucoptera*. Target journal *Emu*

4.2 INTRODUCTION

Division of incubation duties between sexes varies greatly in birds. In many species the female conducts all the incubation whereas in others, such as the cassowaries (*Casuariidae*), only the male incubates (Crome 1976). In some species the parents share incubation duties and each individual has to partition limited resources into reproduction and self-provisioning. Consequently, there is often a conflict between the male and female over the division of labour (Jones et al. 2002).

For Procellariiformes (albatrosses, petrels and shearwaters), total lengths of incubation seem inordinately longer than that of other birds that produce eggs of similar size (Brooke 2004). Incubation is shared by both parents; while one partner incubates the egg, the other returns to sea. Incubating Procellariiformes do not feed while on the nest, so during their time at sea, breeding birds need to forage sufficiently to both meet their immediate nutritional needs and to store body reserves in anticipation of their next incubation shift. If sufficient reserves are not stored, the bird may later desert the nest prematurely, potentially leading to breeding failure (Chaurand & Weimerskirch 1994a). Conversely, spending too much time at sea may delay their return to relieve their partner, increasing the partner's period of fasting and the likelihood that it will abandon the nest (Johnstone & Davis 1990)

Incubation shifts of some Procellariiformes can be extremely long (Warham 1990), consequently breeding birds may endure extended periods of fasting that can lead to significant reductions in body mass. These physiological changes are an important factor in the behavioural decisions of parents attempting to balance their own energy requirements with the embryo's needs for warmth and protection. When incubating shifts are lengthy, there is a greater risk that the sitting bird will reach its physiological limits and return to sea to feed

before its partner returns to take over incubation duties. Such temporary desertions are quite common in pelagic seabirds (Chaurand & Weimerskirch 1994a) and do not necessarily lead to breeding failure (Boersma & Wheelwright 1979). However, abandoning the egg temporarily both reduces the likelihood of hatching by interrupting the incubation process, and increases the risk of predation of the unprotected egg.

Brooke (2004) described behaviour rules that incubating birds might use when deserting: sit until the mate returns, but desert if (a) weight decreases close to some threshold value, or (b) the number of days the bird has been sitting on the egg is clearly longer than the mean shift length. However, the length of incubation shift is governed not by the incubating bird, but by the return-to-the-nest decisions of the mate who is foraging (Dearborn 2001). Therefore, to co-ordinate incubation shifts, birds may need to assess their partner's body condition before they leave the nest.

One way to assess the potential cost of incubation in birds is to monitor the co-ordination of incubation shift and adult body mass (Drent & Daan 1980). For petrels, the mean duration of incubation shifts varies from 2.4 days for Fairy Prions (*Pachyptila turtur*) (Harper 1976) to 16.5 days for Dark-rumped Petrels (*Pterodroma phaeopygia*) (Simons 1985). A major determinant of shift length is body size, with large birds having a greater capacity for fasting than small ones (Warham 1990). Incubation shifts of up to 3 weeks have been observed for Gould's Petrel (*Pterodroma leucoptera*) (225 g; (O'Dwyer 2004), longer than species of similar size such as the Soft-plumed Petrel (*Pterodroma mollis*) (12.5 days, 302 g; (Jouventin et al. 1985), Mottled Petrel (*Pterodroma inexpectata*) (13.1 days, 329 g; (Warham et al. 1977), Snow Petrel (*Pagodroma nivea*) (5.7 days, 330 g; (Isenmann 1970) and Kergulen Petrel (*Lugensa brevirostris*) (13 days, 331 g; (Mougin 1975). The extended periods of fasting

associated with such long incubation shifts must be energetically challenging for Gould's Petrel.

Using data collected during the 1996–97 breeding season, this chapter investigates the incubation routine of the Gould's Petrel and the associated changes in body mass. The specific aims were to: (1) determine the pattern and duration of incubation shifts and the causes of incubation failure; (2) investigate changes in mass of both sexes during incubation; and (3) explore the relationships between body mass, incubation shift duration and nest desertion.

4.3 MATERIALS AND METHODS

Gould's Petrels nest principally within the two steep gullies on the western side of Cabbage Tree Island (CTI) (Figure 1.2, (Fullagar 1976)). Typically, they nest underground in natural cavities within the rock scree, but also occasionally in boulder crevices, hollow fallen palm trunks, among the buttresses of fig trees and under fallen palm fronds (Priddel & Carlile 1997b). Unlike many other small Procellariiformes, Gould's Petrels do not dig earth burrows. Their annual breeding cycle including time of egg laying, hatching and chick rearing is described in Chapter 1.

4.3.1 NEST MONITORING

Monitoring of the Gould's Petrel population between 1992 and 1996 located more than 700 nest sites within their principal breeding habitat (Priddel & Carlile 2007). Adults breeding within these sites had been banded with a numbered metal band provided by the Australian Bird and Bat Banding Scheme.

On 18 November 1996, 250 readily accessible nests that had been occupied during the previous breeding season were inspected. Nests that contained an egg were deleted from the sample because the exact date of laying was unknown. All remaining nests were checked daily for the next 12 days and, for those that subsequently contained eggs ($n = 65$), the date of laying was recorded. Any bird present with the egg was extracted from the nest, identified, weighed, and sexed by cloacal examination (Serventy 1956, O'Dwyer et al. 2006c).

The 65 nests containing eggs of known age were then inspected daily until 17 January 1997 or until the egg failed; i.e., were predated, broken or permanently abandoned. At each inspection, the condition of the egg (damaged or undamaged) or chick (alive or dead) was assessed and the adult in attendance was identified and weighed. If the egg is damaged, it was assumed that the egg was damaged by the adult in the nest. However, if change of shift happened on the day when the damage was found, the bird who damaged the egg was recorded as unknown. Occasionally the adult retreated deep into the nest cavity and could not be reached, so some weights were missed. Newly hatched chicks were weighed, but not disturbed again during the guard stage; i.e., until the adult was no longer in attendance (1–2 days). Unattended chicks were weighed daily. Nests were inspected again during 7–9 March 1997 and the presence of an advanced chick recorded.

4.3.2 STATISTICAL ANALYSES

Statistical analyses were conducted using IBM SPSS version 21. A Chi-square test was used to determine whether the number of damaged eggs varied between sexes. Pearson's correlation coefficients were used to test for associations between variables. Student's t-tests (independent) or Analyses of Variance (ANOVA) were used to test for differences between incubation shifts and between completed and abandoned shifts. Where the assumptions of

these tests were not met, the non-parametric equivalents were used. The significance criterion for all tests was set at < 0.05 . All data are presented as means \pm standard deviation.

4.4 RESULTS

4.4.1 EGG LAYING

Egg laying occurred between 18 and 28 November (Figure 4.1). The mean date of laying was 23 November \pm 2.9 days ($n = 65$), with no difference in laying date between those eggs that hatched successfully and those that failed (Mann-Whitney U test, $U = 515.0$, $P = 0.895$).

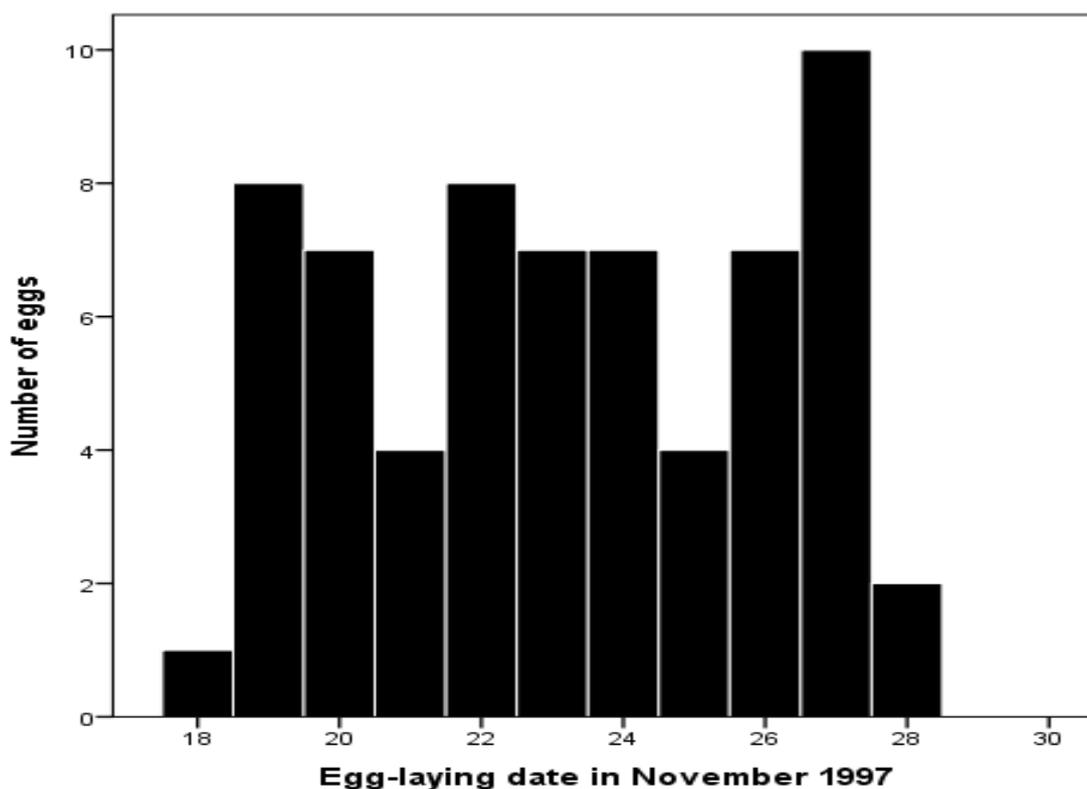


Figure 4.1 Date of egg laying for the 65 monitored Gould's Petrel nests.

4.4.2 HATCHING SUCCESS

From the 65 nests monitored, 30 eggs hatched successfully and two died while hatching. The mean incubation period was 48.2 ± 1.5 days ($n = 32$; excluding days when eggs were temporarily abandoned), and the range 45–52 days. Another four breeding pairs incubated for at least 45 days (48, 49, 50, and 50 days), but the eggs failed to hatch. Although hatching failed at these four nests the parents were considered to have completed incubation and were included in the analysis of incubation routines.

Twenty-nine pairs failed to complete incubation (i.e., parents sat for < 45 days). Reasons for incubation failure were egg damage (83%) and desertion of intact eggs by parents (17%). Of the 24 damaged eggs, 15 were damaged when the male was in attendance, seven eggs were damaged when the female was present, and two occurred during changeovers and could not be assigned to either sex. The number of damaged eggs was not significantly different between sexes (one sample binomial test = 15, SE = 2.35, $P = 0.13$), and the rate of egg damage (eggs damaged per 100 days sitting) was 0.174 for males and 0.141 for females.

4.4.3 CHICK SURVIVAL

One chick was found dead 3 days after hatching; the cause of death is unknown. The remaining 29 chicks were alive and well in March 1997 and are presumed to have fledged, as mortality of well-advanced chicks is rare (Priddel et al. 1995).

4.4.4 INCUBATION ROUTINE

Males typically undertook the greater proportion of incubation duties (mean: males 63.5% *cf.* females 36.5%; Z test, $Z = 11.23$, $P < 0.01$). However, the variation in this proportion (males: 50.0–69.7%) suggests a high degree of flexibility in incubation schedules. Incubation was completed in three (33% of nests), four (53%) or five (14%) shifts (Figure 4.2). Most

incubation took place during three long incubation shifts (hereafter Shifts 1, 2 and 3; Table 4.1), the male undertaking the first and third (mean 16.6 ± 2.5 days and 13.7 ± 2.3 days, respectively), and the female the second (mean 15.6 ± 1.7 days). The duration of these three shifts was significantly different (ANOVA, $F_{2, 33} = 16.9$, $P < 0.001$), each one being shorter than its predecessor. In 36% of nests, the female undertook a short incubation shift (mean 2.2 ± 1.3 days) immediately after egg laying (hereafter Shift 0, Figure 4.2). In 44% of nests, the female undertook a short shift (mean 2.7 ± 2.2 days) of variable length (1–8 days) at the end of incubation immediately prior to hatching (hereafter Shift 4, Figure 4.2). Five females (14%) undertook both the initial and final shift (Shifts 0 and 4, Figure 4.2). Shifts 1, 2 and 3 were shorter for failed breeders than for successful breeders, whereas the duration of Shifts 0 and 4 were independent of success or failure (Table 4.1). The maximum incubation shift recorded was 22 days.

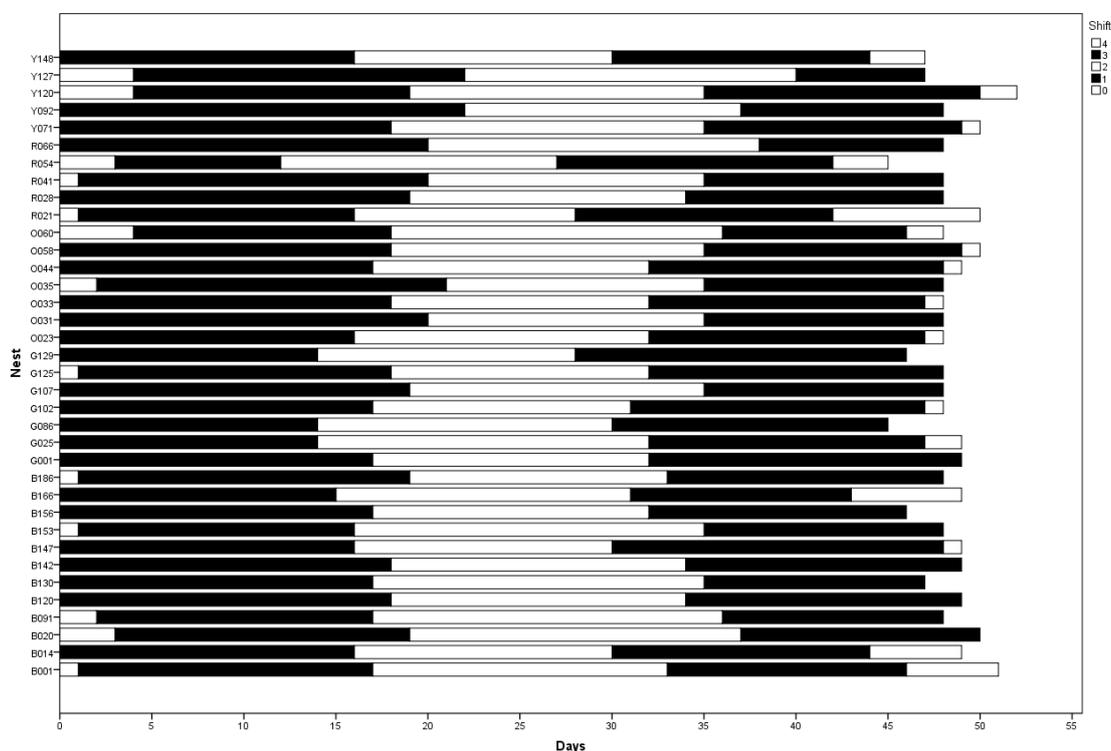


Figure 4.2 Incubation shifts undertaken by male (solid bars) and female (open bars) Gould's Petrel.

Table 4.1 Duration of each incubation shift for Gould's Petrel pairs that (a) successfully completed incubation and (b) failed. Data are means \pm SD, with ranges in parentheses.

| Shift | Sex | Successful | | Failed | | <i>t</i> | <i>P</i> |
|-------|-----|------------|------------------------|----------|-----------------------|----------|----------|
| | | <i>n</i> | Length (days) | <i>n</i> | Length (days) | | |
| 0 | F | 13 | 2.2 \pm 1.3 (1–4) | 13 | 2.2 \pm 1.5 (0–5) | 0.000 | 1.00 |
| 1 | M | 36 | 16.7 \pm 2.3 (9–22) | 26 | 14.0 \pm 4.5 (1–21) | 3.048 | < 0.01 |
| 2 | F | 36 | 15.6 \pm 1.7 (12–19) | 21 | 11.7 \pm 4.8 (1–17) | 4.436 | < 0.01 |
| 3 | M | 36 | 13.9 \pm 2.1 (7–18) | 16 | 7.2 \pm 4.9 (1–16) | 7.025 | < 0.01 |
| 4 | F | 16 | 2.7 \pm 2.2 (1–8) | 4 | 4.3 \pm 2.1 (2–6) | 1.292 | 0.21 |

4.4.5 NEST DESERTION

Overall, there were 25 instances of desertion of intact eggs (ie. no visible damages found) among the 65 nests monitored; 5 were permanent (i.e., neither parent returned to resume incubation) and 20 were temporary (i.e., at least one parent returned and resumed incubation). Most ($n = 21$) desertions involved unsuccessful nests, although four temporary desertions (for periods of one day only) involved nests that successfully hatched eggs (Figure 4.2). Of these, one nest was abandoned by the male for a single day near the end of Shift 3. The male returned the following day and sat for one more day until relieved by the female. A second nest was temporarily abandoned at the end of Shift 1 (15 days into incubation), with the male leaving a day before the female returned. Another nest was abandoned twice, first, by the female during Shift 2, after sitting for 14 days. The female came back the next day and incubated for a further four days before being relieved by the male. Nine days later, the male also abandoned this nest, returning after a single day to sit for another day until relieved by the female.

Incubation shifts that were abandoned (either temporarily or permanently, $n = 25$) were compared with completed shifts (i.e., the incubating bird stayed until its partner returned, $n = 173$). The duration of abandoned shifts was significantly shorter than completed shifts for

Shift 1 and Shift 2, near-significantly shorter for Shift 3 ($P = 0.07$), but similar for Shift 4 (Table 4.2). There was no difference in desertion rate between males (64%) and females (36%) (Z test for proportion, $Z = 1.4$, $P = 0.16$).

Table 4.2 Duration of each incubation shift for incubating Gould’s petrels that (a) were relieved by partner, and (b) abandoned. Data are means \pm SD, with ranges in parentheses.

| Shift | Sex | Relieved | | Abandoned | | <i>t</i> | <i>P</i> |
|-------|-----|----------|-----------------------|-----------|-----------------------|----------|----------|
| | | <i>n</i> | Length (days) | <i>n</i> | Length (days) | | |
| 0 | F | 24 | 2.9 \pm 4.0 (1–21) | 1 | 2.0 | | |
| 1 | M | 52 | 16.4 \pm 2.3 (9–22) | 6 | 7.8 \pm 5.4 (1–15) | 3.852 | 0.011 |
| 2 | F | 46 | 15.0 \pm 2.5 (7–19) | 6 | 12.0 \pm 4.2 (4–16) | 2.571 | 0.013 |
| 3 | M | 35 | 13.6 \pm 2.5 (5–18) | 10 | 10.8 \pm 4.1 (5–18) | 2.007 | 0.070 |
| 4 | F | 16 | 3.0 \pm 2.3 (1–8) | 2 | 3.5 \pm 3.5 (1–6) | 0.280 | 0.783 |

4.4.6 CHANGES IN BODY MASS

Incubating birds underwent substantial changes in body mass. On average, male body mass reduced from 240.7 \pm 16.4 g at the start of Shift 1 to 183.8 \pm 15.5 g at the conclusion of Shift 3; a loss of 56.9 g or 23.6% of starting body mass. Males that completed Shift 1 were on average 13.2 g lighter at the start of Shift 3 than at the start of Shift 1 (paired t-test, $t = 7.443$, $df = 35$, $P < 0.000$). However, weights at the finish of these shifts were similar (paired t-test, $t = -0.452$, $df = 35$, $P = 0.654$).

Females lost body mass through both egg laying and incubation, but because females were not captured prior to egg laying only losses due to incubation were recorded. Females were lightest immediately after egg laying (Shift 0) but regained considerable weight (mean increase 40.8 \pm 11.0 g) by the start of their long incubation shift (Shift 2), the difference being significant (paired t-test, $t = 13.344$, $df = 12$, $P < 0.001$). Females lost an average of 22.1 \pm 10.1 g between the start of Shift 2 and Shift 4 (paired t-test, $t = 8.701$, $df = 15$, $P < 0.001$).

Body mass of males at the start of Shift 1 and Shift 3 was less for abandoned shifts than for completed shifts (Table 4.3), but there was no difference between abandoned and completed shifts in body mass at the finish of these shifts (Table 4.4). In contrast, body mass of females at the start of Shift 2 was similar for abandoned and completed shifts (Table 4.3), but at the finish of the shift body mass was less for abandoned shifts than for completed shifts (Table 4.4).

Table 4.3 Body mass at the start of each incubation shift for Gould's Petrel pairs that (a) were relieved by their partner or (b) abandoned. Data are means \pm SD, with ranges in parentheses.

| Shift | Sex | Relieved | | Abandoned | | <i>t</i> | <i>P</i> |
|-------|-----|----------|----------------------------|-----------|----------------------------|----------|----------|
| | | <i>n</i> | Body mass (g) | <i>n</i> | Body mass (g) | | |
| 0 | F | 24 | 194.8 \pm 14.5 (172–245) | 1 | 239.0 | | |
| 1 | M | 52 | 240.0 \pm 15.1 (212–280) | 6 | 216.7 \pm 15.4 (199–234) | 3.566 | 0.001 |
| 2 | F | 46 | 229.5 \pm 13.3 (182–259) | 6 | 214.7 \pm 24.1 (176–244) | 1.478 | 0.195 |
| 3 | M | 35 | 228.5 \pm 14.0 (200–252) | 10 | 217.0 \pm 18.1 (183–242) | 2.134 | 0.039 |
| 4 | F | 16 | 207.8 \pm 9.9 (189–232) | 2 | 214.5 \pm 17.7 (202–227) | -0.852 | 0.407 |

Table 4.4 Body mass at the finish of each incubation shift for Gould's Petrel pairs that (a) were relieved by their partner, or (b) abandoned. Data are means \pm SD, with ranges in parentheses

| Shift | Sex | Relieved | | Abandoned | | <i>t</i> | <i>P</i> |
|-------|-----|----------|----------------------------|-----------|----------------------------|----------|----------|
| | | <i>n</i> | Body mass (g) | <i>n</i> | Body mass (g) | | |
| 0 | F | 24 | 187.7 \pm 12.4 (159–214) | 1 | 230.9 | | |
| 1 | M | 52 | 182.0 \pm 14.7 (151–218) | 6 | 189.2 \pm 25.1 (152–230) | -1.043 | 0.302 |
| 2 | F | 46 | 178.8 \pm 12.8 (151–208) | 6 | 167.8 \pm 7.6 (156–176) | 2.031 | 0.048 |
| 3 | M | 35 | 185.9 \pm 16.6 (154–227) | 10 | 176.1 \pm 16.0 (155–202) | 1.665 | 0.103 |
| 4 | F | 16 | 199.4 \pm 14.0 (178–227) | 2 | 202.5 \pm 0.7 (202–203) | -0.301 | 0.767 |

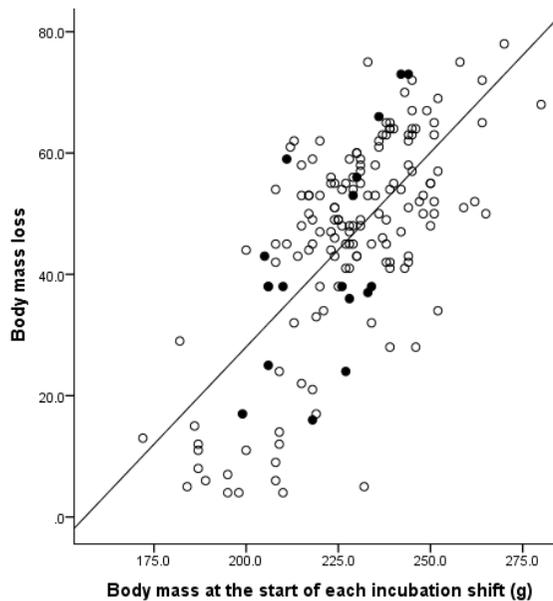
For birds that completed incubation the rate of weight loss differed among incubation shifts (ANOVA, $F_{4, 117} = 5.814$, $P < 0.001$), with considerably lower rates during the two shorter shifts (Shifts 0 and 4). Excluding the two short shifts daily weight loss was significantly different (Shifts 1–3; ANOVA, $F_{2, 105} = 5.441$, $P = 0.006$; Table 4.5), with loss during Shift 3

lower than during Shift 1. On average, the mass lost during each long shift was equivalent to 19–24% of starting body mass (Table 4.5). Actual weight loss, proportional weight loss and the rate of weight loss were all positively correlated to body mass at the beginning of the shift, with heavier birds tending to lose more weight (Figure 4.3). There was no discernible difference in actual, proportional, or daily weight loss between birds that completed incubation shifts and those that abandoned (Figure 4.3). There was only a weak positive correlation between body mass at the start of each incubation shift and length of the shift ($y = 0.03x + 7.74$, $r_{106} = 0.195$, $P = 0.43$, $R^2 = 0.038$).

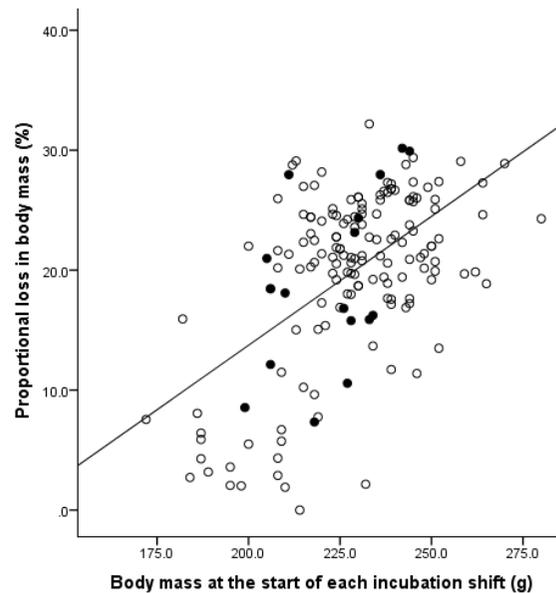
Table 4.5 Loss of body mass during each incubation shift for Gould's Petrel pairs that completed incubation. Data are means \pm SD, with number of samples in parentheses.

| Shift | Sex | Mass loss (g) | Proportional loss (%) | Rate of loss (g day ⁻¹) |
|-------|-----|----------------------|-----------------------|-------------------------------------|
| 0 | F | 8.8 \pm 4.4 (6) | 4.6 \pm 2.4 | 2.7 \pm 0.6 |
| 1 | M | 58.2 \pm 9.4 (36) | 24.2 \pm 3.8 | 3.5 \pm 0.4 |
| 2 | F | 51.8 \pm 7.6 (36) | 22.4 \pm 3.1 | 3.3 \pm 0.3 |
| 3 | M | 43.9 \pm 10.6 (36) | 19.2 \pm 4.4 | 3.2 \pm 0.5 |
| 4 | F | 13.0 \pm 9.9 (8) | 6.2 \pm 4.7 | 2.9 \pm 1.1 |

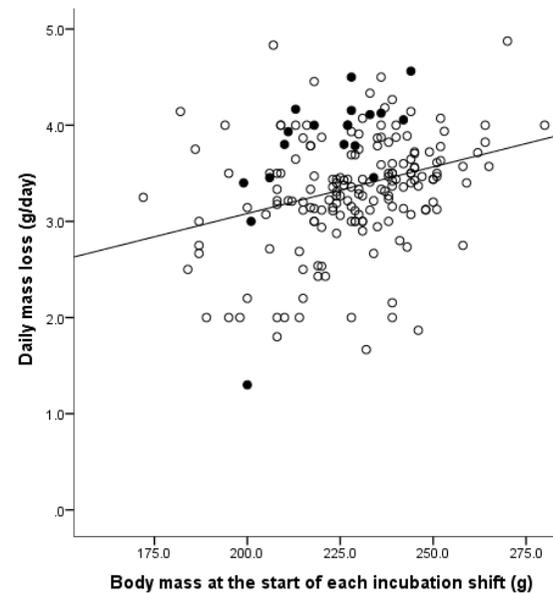
The longer birds were at sea, the heavier they returned ($r_{104} = 0.369$, $P < 0.001$, $R^2 = 0.136$; Figure 4.4). However, time spent at sea was not related to mass gained at sea ($r_{94} = 0.181$, $P = 0.081$). Mass gain at sea averaged 40.3 ± 15.5 g (range -15–71 g, $n = 94$) or 2.7 ± 1.3 g day⁻¹ (range -3.8–6.6 g, $n = 94$), and was inversely related to body mass at the time of departure ($r_{94} = -0.446$, $P < 0.001$; Figure 4.5).



A



B



C

Figure 4.3 The relationship between body mass of Gould's Petrel at the start of each incubation shift and: (A) Actual body mass loss ($y = 0.64x - 0.01$, $R^2 = 0.461$); (B) proportional loss ($y = 0.21x - 29.24$, $R^2 = 0.304$); (C) daily mass loss ($y = 0.0097x + 1.14$, $R^2 = 0.084$); for birds that abandoned their egg (closed circles) and those that stayed until relieved by their partner (open circles).

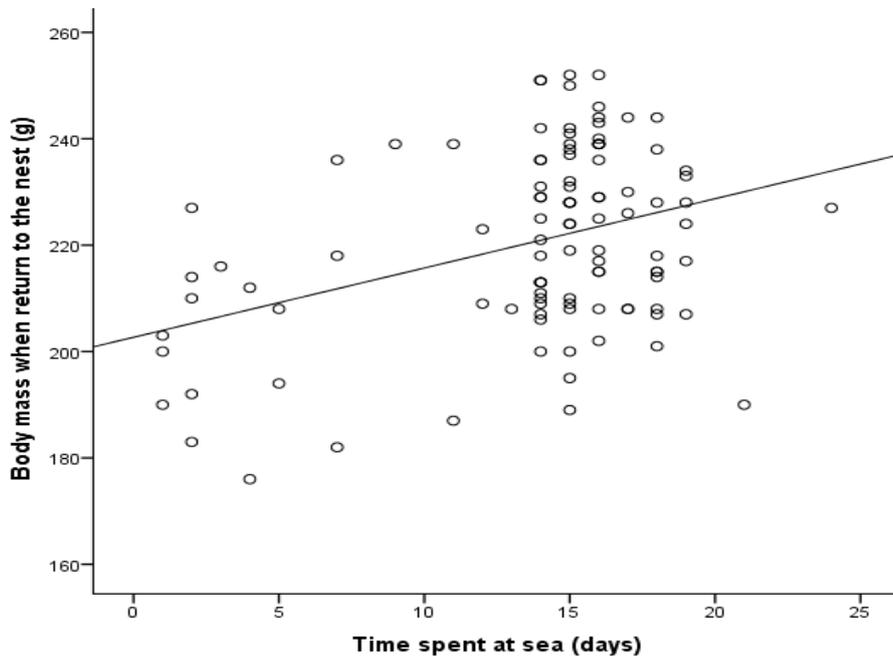


Figure 4.4 The relationship between time spent at sea by Gould's Petrels during incubation and body mass on return ($y = 1.3x + 203$, $R^2 = 0.136$).

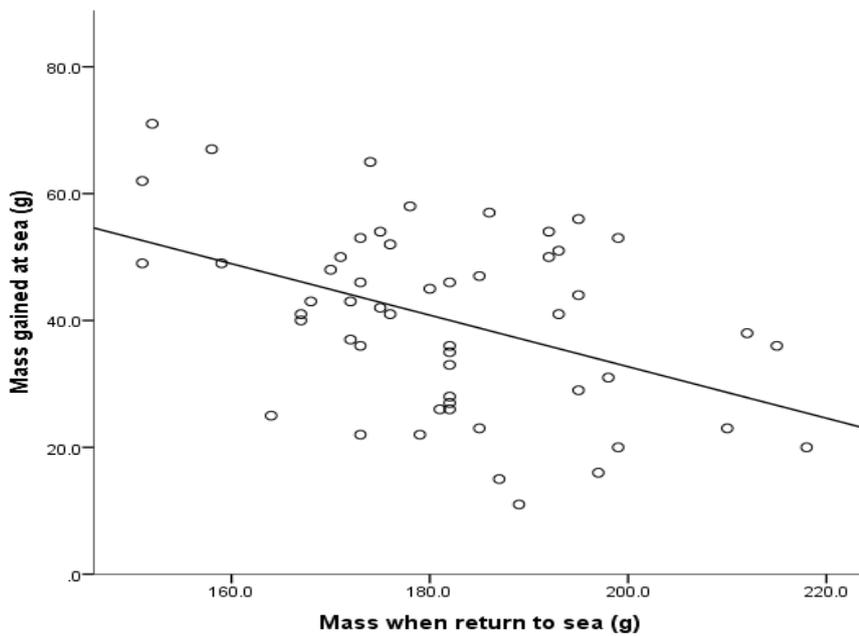


Figure 4.5 The relationship between body mass of Gould's Petrels at the finish of an incubation shift and body mass gained at sea ($y = 114 - 0.41x$, $R^2 = 0.188$).

4.5 DISCUSSION

This chapter provides the first detailed account of the incubation routine of Gould's Petrel, which was found to be similar to that of other Procellariiformes (see review by Warham 1990). After laying in mid-late November, the female typically departed the nest immediately, although the absence of their mate sometimes delayed their departure a day or two. Invariably, the male was responsible for the first long incubation shift. The female then undertook the second long shift, with the male returning to do the third. The female sometimes returned before hatching to undertake a short and final incubation stint. This final changeover, at or near the time of hatching, may help to ensure that the parent in attendance has food for the new hatchling. Peeping (calling from within the egg) by chicks for several days before hatching might also be a cue for both parents to shorten their off-duty periods (Warham 1996).

The duration of each shift lessens over the incubation period (Table 4.1). Parents undergo a substantial decline in body mass between laying and hatching, and the decrease in shift length over the course of incubation may reflect a reduction in the birds' ability to fast for extensive periods. Alternatively, the chick-rearing period is often timed to coincide with when food is most locally abundant (Warham 1996) and declining shift length may reflect food becoming increasingly more available closer to the colony.

Like other Procellariiformes, Gould's Petrels lay relatively large eggs (mean 39.6 g, $n = 195$; (O'Dwyer 2004) compared to body size, consequently the energy requirements for egg formation are high. The female is at her minimum weight immediately after laying, and in need of replenishing her body reserves. Consequently the male undertakes the first major incubation shift. The long duration of this initial shift (mean 16.6 days, $n = 52$) provides the

female with a relatively long time to recover body condition. Males spend more time incubating than females (mean 31.1 days *cf.* 17.8 days), presumably to compensate for the females energy contribution to egg formation. Such biparental care is an evolutionarily stable strategy whereby each parent partially compensates for any decrease in effort by the partner (Houston & Davies 1985).

The incubation period for Gould's Petrel was 48.2 ± 1.5 days ($n = 32$). Warham (1996) demonstrated that the incubation period (p) of petrels is a function of body mass (m). This relationship ($p = 26.33m^{0.116}$) predicts an incubation period for Gould's Petrel of 49.2 days, similar to that observed. Thus, the incubation period for Gould's Petrel is similar to that of other similar-sized petrels.

4.5.1 INCUBATION SUCCESS AND CAUSES OF FAILURE

Breeding success (the proportion of eggs that produced advanced chicks) during this study was 45%, similar to other years (mean 49.4%, range 25.5–58.6% between 1993–94 and 2005–06; Priddel & Carlile (2007)). Also consistent with other years, most chicks that hatched survived to fledging (97%, $n = 30$), with the single death occurring within three days of hatching. The cause of death is unknown, but it seemed to be associated with the absence of both parents during the guard stage. Death of unattended newly hatched chicks is not uncommon among seabirds. Fork-tailed Storm-petrel (*Oceanodroma furcata*) chicks die if deserted by their parents before their down is dry (Simons 1981) and Little Penguin (*Eudyptula minor*) chicks die if not fed within three days after hatching (Renner 1998). Laying date is known to effect breeding success in a number of petrel species, such as Manx Shearwater (*Puffinus puffinus*) (Perrins 1966) and Wilson's Storm-petrel (*Oceanites oceanicus*) (Quillfeldt 2001). Sampled eggs were from only the peak laying period (18–28

November) during which approximately 80% of eggs are laid (O'Dwyer 2004), but I found no evidence that the date of laying affected breeding success. O'Dwyer (2004) studied Gould's Petrel eggs throughout the entire laying period (up to 21 December) but also found no relationship between laying date and breeding success.

Hatching success (the number of eggs that produced chicks) was 49%, less than that reported for Gould's Petrel by O'Dwyer (2004)—76% in 2001/02 and 65% in 2002/03. However, O'Dwyer (2004) selectively studied only established pairs with a history of successful breeding. In my study, the primary cause of hatching failure (83%, $n = 29$) was physical damage to the egg resulting in cracking or breakage. The rate of egg breakage was similar for males and females. The extreme rocky nature of the nesting habitat on CTI no doubt contributes to the high rate of egg breakage. Providing soft materials inside the artificial nest boxes should be considered as a conservation method to improve reproductive success of the species.

The secondary cause of hatching failure (17%, $n = 29$) was nest desertion by the parents. For the egg to hatch successfully, each partner needed to return in time to relieve one another from incubation duties. Three pairs managed to hatch their egg despite temporary breaks in incubation caused when the sitting bird left before its partner returned. However, none of these breaks exceeded one day. Eggs that were abandoned for longer than one day ($n = 5$), all failed to hatch. Thus, although Gould's Petrel eggs are resilient to short breaks in incubation, longer breaks appear fatal. The possible exception here is of eggs that are close to hatching, as eggs of this age are partially resistant to chilling due to their ability to generate their own heat. This finding combined with the mass at the beginning of an incubation shift suggests that it

should be possible to determine if a bird will likely get into food stress and depart before the partner returns or have to top up reserves with a one day trip.

Nest desertion has been reported to be a major cause of nesting failure in many petrels (Weimerskirch et al. 1989); for example, it was purported to be the prime cause of egg failure in the Grey-faced Petrel (*Pterodroma macroptera gouldi*) (Johnstone & Davis 1990). However, it is possible that many desertions occur when the parents senses the egg is no longer viable. Although, nearly half (45%, 29 eggs out of total 65 eggs) of the Gould's Petrel eggs were eventually abandoned, most desertions (79%, 23 eggs out of 29 eggs abandoned) occurred only after the egg was damaged. Intact eggs that were abandoned ($n = 5$) died either because of damage sustained while the egg was unattended or through prolonged chilling.

On average, nest desertions occurred before the normal duration of the incubation shift (Table 4.1) suggesting that birds that deserted left early and, thus, abandonment of the egg was not due to excessively long shifts caused by the late return of the partner. Also, the body mass of males that abandoned was no less than that of those that stayed until relieved (Table 4.4); again suggesting that excessive fasting was not the trigger for their early departure. Those males that deserted the nest were of lower body mass at the start of the incubation shift and so were seemingly ill prepared to endure the period of fasting necessary to complete their shift. These individuals may have been young birds or inexperienced breeders, which have a lower rate of breeding success than established breeders (Warham 1990).

Prolactin is believed to be the hormone responsible for promoting incubation behaviour in birds (O'Dwyer et al. 2006b), and males, with lower levels of prolactin and higher levels of testosterone than females, may be more inclined to abandon the egg (O'Dwyer 2004). Nest desertions by the Grey-faced Petrel more often involved males than females (Johnstone &

Davis 1990). However, I found no statistical difference in the desertion rate of male and female Gould's Petrel. Males that abandoned intact eggs had a lower body mass at the *beginning* of the shift than those that stayed until relieved by their partner, whereas females that abandoned had a lower mass at the *conclusion* of the incubation shift. This distinction may indicate that different factors influence the incubation behaviour and associated decision making of each sex. However, there was no evidence that weight loss during incubation or weight gained at sea differed between the sexes.

At least three Gould's Petrel nests were attended by more than two birds. At one nest, a female laid and departed immediately. A second female incubated this egg (or perhaps destroyed the first egg and laid a replacement) for two days until the male arrived to take over incubation. The initial female was not seen again and the egg hatched successfully. However, the other two nests failed. One egg was damaged; the other was repeatedly abandoned. More than a single pair of Gould's Petrel attempting to use the same nest site is not uncommon, having been observed frequently during routine monitoring of the population (Priddel & Carlile 2007). However, Gould's Petrel nests with two eggs are rarely successful. Territorial disputes often result in the eggs getting damaged, and in the case where eggs remain undamaged, each is usually only partially incubated.

4.5.2 LENGTH OF INCUBATION SHIFTS

A major determinant of the length of incubation shifts is body mass, because larger birds have a greater capacity for fasting than smaller ones. In species where the sexes differ in size, the heavier sex tends to sit longer (Warham 1990). Gould's Petrel has a relatively long incubation shift for its size. Other small Cookilaria petrels, the closest relatives of the Gould's Petrel, also have long incubation shifts for their size (10–14 days, mass 160–200 g; Rayner et al. 2012).

More broadly, Gadfly petrels (of the genus *Pterodroma*) generally have incubation shifts that average 13–19 days (Brooke 2004) with other subtropical or tropical species such as Hawaiian Petrel (*P. phaeopygia*), Juan Fernandez Petrel (*P. externa*) and Murphy's Petrel (*P. ultima*) among those at the upper end of the range (Simons 1985, Brooke 1987, 1995). Long incubation shifts have the advantage of minimising the number of changeovers, which can be a major cause of nesting failure for some petrels (Weimerskirch et al. 1989). Long incubation shifts are energetically taxing, but free the partner to forage for longer and to go further afield. In Chapter 5, foraging behaviour studied by geolocation loggers indicates that Gould's Petrels breeding on CTI forage predominately in the western Tasman Sea, up to 2000 km away. Foraging capabilities are presumably linked with age (Ryder 1980, Duffy 1983, Greig et al. 1983) and incorporating investigations into how age and experience affect foraging outcomes is likely to greatly enhance our understanding of seabird foraging ecology and its interactions with breeding success.

4.5.3 BODY MASS CHANGES

The rate of mass loss by fasting birds during incubation is a reliable index of energy cost and correlates well with body mass, being relatively high in small species (Croxall 1982). Reported daily losses range from approximately 6.0% of initial body mass for small storm petrels, to 2.0% in medium-sized shearwaters, and only 0.8% in the large albatrosses (see Table 3 in Weimerskirch 1989). Compared to other species, Gould's Petrel has a higher proportional loss of mass than other petrels with similar incubation shifts. The corollary is that petrels that have a similar rate of mass loss to Gould's Petrel have much shorter incubation shifts. Thus, it is remarkable that Gould's Petrel can incubate for such a long period and tolerate such a high rate of mass loss. The composition of body mass lost during

fasting (either water, fat or protein) is highly variable between birds (Croxall 1982) and it is possible that much of the mass lost by Gould's Petrels is water rather than fat or protein. This possibility is consistent with the observation that the rate of mass loss was positively correlated to body mass at the beginning of the shift, with heavier birds tending to lose mass faster.

There was only a weak positive relationship between length of the incubation shift and body mass at the start of the shift ($R^2 = 0.038$) presumably because the timing of the changeover is driven by the return of the partner rather than the condition of the incubating bird. Also, the inverse relationship between body mass at the finish of an incubation shift and body mass gained at sea indicates that breeding birds that lost excessive mass were able to regain much of that mass whilst at sea. These two findings support the belief that food resources are not limiting the breeding success of Gould's Petrel, at least during the particular year that these data were collected (1996–97). Since 1993–94 there has been only one year of exceptionally poor breeding success. In this year (1995–96), poor breeding success of Gould's Petrel on CTI was coincident with the widespread mortality of Pilchards (*Sardinops sagax*) within southern Australian and New Zealand waters (Ward et al. 2001), which was thought to be caused by the introduction of a herpes virus in fish imported as feed for fish farms (Jones et al. 1997). Little Penguins (*Eudyptula minor*) in Port Phillip Bay, Victoria, also experienced a high incidence of egg abandonment and unusually poor breeding success during the 1995–96 breeding season (Dann et al. 2000). If such a drastic decline in Gould's Petrel breeding success were to recur, it would be informative to reconstruct the relationship between mass gain at sea and body mass at the time of departure (as per Figure 4.5) and compare the slope of the regression line with that observed in this study.

5 CHAPTER 5 – FORAGING BEHAVIOUR, DIET AND NEST ATTENDANCE OF GOULD’S PETREL DURING BREEDING⁴

5.1 ABSTRACT

Many pelagic seabirds are central place foragers and adopt a dual foraging strategy in the breeding season, with adults alternating short and long trips when provisioning chicks. I investigated foraging cycles in the threatened Gould's Petrel (*Pterodroma leucoptera*) over the 2010–2011 and 2011–2012 breeding seasons by quantifying foraging movements and associated behaviours in relation to reproduction. Kernel density models derived from geolocator data showed an extensive foraging range off south-eastern and southern Australia and differences in foraging locations during incubation: (a) with season; and, (b) between sexes. Core foraging areas were characterised by low concentration values of chlorophyll *a*, warm sea-surface temperature and deep waters. Monitoring of nest attendance revealed 24 - 37 % of all trips were between 1–2 days in duration, and 11–14% of trips were between 3–5 days. Meal size of the provisioned chick increased with increasing trip duration, but did not differ between male and female parents. Finally, I assessed dietary diversity by sampling regurgitated adult and chick stomach contents. Analyses revealed high frequencies of fish, cephalopods and crustaceans, with some variation within and between seasons in all three categories. This variation in diet is important for Gould’s Petrel, a species that forages in highly variable environments.

⁴ Kim, Y., Priddel, D., Grech, A., Merrick, J.R., Carlile, N. and Harcourt, R. *In prep.* Foraging behaviour, diet and nest attendance of Gould’s Petrel during breeding. Target journal *Marine Ecology Progress Series*

5.2 INTRODUCTION

The distribution and abundance of food resources for top marine predators varies both in time and space (Quillfeldt et al. 2010). For seabirds exposed to this variation, flexible foraging behaviour is critical to their survival (Rayner et al. 2010). Procellariiformes (albatrosses, shearwaters and petrels) are wide-ranging, pelagic seabirds with adaptations that confer the ability to cover long distances and/or large areas in search of prey (Croxall 1987, Pennycuik 1987). They feed upon patchily distributed marine prey and travel long distances before returning to their breeding location (Phillips et al. 2005, Weimerskirch et al. 2007).

Studies of the foraging behaviour of seabirds during the breeding season find clear links between prey availability and predator reproductive success (Hamer et al. 2007). Breeding seabirds are central place foragers, commuting between their colonies and pelagic feeding zones to feed their chicks (Ropert-Coudert et al. 2004). They also switch from feeding only themselves to feeding themselves and the chick at the same time (Paiva et al. 2010). While provisioning chicks, there are time constraints on how long and how far seabirds can travel to forage as the chicks must fast while the parents are at sea. The identification of core foraging areas and information on how pelagic seabirds use these foraging areas is integral to understanding the strategies to balance resource constraints with reproductive success (Phillips et al. 2006). Many Procellariiformes are known to adopt a dual foraging strategy; the parents alternate or mix short trips over the waters surrounding colonies to provide food for chicks with long foraging trips to more productive distant areas to restore their own body reserves (Congdon et al. 2005, González-Solís et al. 2007, Welcker et al. 2012). Despite observations of alternation of long and short duration foraging trips by many Procellariiformes, there is often a lack of concurrent behavioural data to evaluate whether

males and females use different marine habitats or have different activity patterns while conducting long and short trips.

Diet studies of seabirds provide information on the prey choice of seabirds (Duffy & Jackson 1986) and changes in diet often reflect changes in the prey base (Montevecchi & Myers 1995). Very little is known about the prevalence of the dual foraging strategy and diet of Gould's Petrel. Marchant and Higgins (1990) suggested that Gould's Petrel eat squid, while Imber (1996) reported finding otoliths of the lantern-fish (*Electrona rissoi*) in the stomach of a single Gould's Petrel found off north New Zealand. McGee (2009) reported 16 genera of cephalopods, at least 3 genera of fish (from 2 families) and some crustaceans in the stomach contents of 88 individuals, and suggested that Gould's Petrels are opportunistic feeders. Extrapolating possible foraging locations from the known ranges of these prey species, McGee (2009) concluded that the Gould's Petrel likely spent this period foraging in coastal areas of the south-western Tasman Sea, possibly near Tasmania.

The goal of this chapter is to investigate variation in foraging areas and prey species of Gould's Petrel within and between breeding seasons. To achieve this goal, I used multiple techniques to: (a) investigate key foraging areas of Gould's Petrel over the incubation and chick rearing period via geolocators; (b) examine the stomach contents of adults and chicks; (c) monitor adult nest attendance by measuring body mass of both adults and chicks, as well as other direct and indirect methods; and, (d) test whether there is a sex difference in foraging behaviour of this monomorphic species. I conclude this chapter with a discussion on the relationship between foraging and breeding behaviour, and associate movements with broad scale oceanographic features.

5.3 MATERIALS AND METHODS

5.3.1 GEOLOCATOR TRACKING AND SPATIAL ANALYSIS

I assessed the movement of Gould's Petrel at sea using 40 Lotek geolocators and 40 Staroddi DST bird geolocators in the 2010–11 and 2011–12 breeding seasons, respectively. Lotek loggers were attached with Darvic rings and Staroddi loggers were attached by Velcro tape, both deployed on the tarsi. The detailed attachment method is described in Chapter 2 and Kim et al. (2014). The attachment of geolocators to Gould's Petrel had no noticeable negative impact on the birds (Kim et al. 2014). The Lotek loggers have an external interface to connect to a computer. Whilst the adult was placed in a cloth bag, data were downloaded without detaching the logger from the bird. During this time, only dim light or red light was used to minimise disturbance to the bird. To download data from Staroddi tags, the tag had to be inserted into a communication box, so these tags were left on the birds and data not retrieved until the end of the breeding season. Both logger models were programmed to record light levels and temperature every 7 minutes, and hence are directly comparable. In addition to light and temperature recorders, the Lotek geolocators were fitted with a wet/dry recorder. Wet/dry status was used to calculate the proportion of time spent in the water. Calculation for daylight was weighted by the latitude of the day.

Lotek geolocators process light level data within the unit to give one spatial location per day. Light data retrieved from Staroddi loggers were processed using the 'tripEstimation' package in R (Sumner 2013). The primary location for each twilight period was estimated using a Bayesian method (Sumner et al. 2009). Locations that required unrealistic flight speeds ($>40 \text{ km h}^{-1}$) and locations that occurred over land were omitted from the analysis. Latitude cannot

be computed from light data around the time of the equinox so these data (equinox date -10 days and + 7 days) were excluded from the analysis.

Foraging areas were identified by generating kernel density maps in R using the packages *sp* (Pebesma et al. 2014), *maptools* (Bivande et al. 2014b), *rgdal* (Bivande et al. 2014a), *adehabitat* (Calenge 2014) and *geosphere* (Hijmans et al. 2014). The kernel density analysis estimated the utilisation distribution (UD); the probability distribution defining the animals' use of space (Fieberg et al. 2005). Kernel density analyses were conducted using location data during the incubation period and the chick rearing period in both 2011 (n = 29) and 2012 (n = 15). To test sex differences in foraging locations, kernel density analysis was conducted using the location data of males (n = 15 in 2011 and n = 5 in 2012) and females (n = 11 in 2011 and n = 7 in 2012). Kernel density analysis was also conducted using location data from different months (January, February and March) during the chick rearing period. The kernel density outputs generated in R were imported to ESRI® ArcGIS™ 10.1 for spatial analysis using an Equidistance Cylindrical projected coordinate system. Kernel density layers were overlaid on maps of sea surface temperature (SST) (in °C, <https://climatedataguide.ucar.edu/climate-data/sst-data-noaa-extended-reconstruction-ssts-version-3-ersstv3-3b>), chlorophyll *a* concentration (Chl *a*, in mg/m³) (<http://hermes.acri.fr/GlobColour/index.php>) and bathymetry (<http://www.ngdc.noaa.gov/mgg/global/global.html>). Core foraging areas were regarded as 50% kernel density contours. Data from the three environmental variables were extracted at a 30 kilometre scale and differences between years were assessed by Mann-Whitney U test in IBM SPSS version 21.

5.3.2 MONITORING NEST ATTENDANCE

Nest attendance was monitored at 20 active nest boxes during 26 December 2010 - 10 January 2011, 8–15 February, 5–9 March and 10–22 April 2011 and from 30 December 2011, 5–14 and 19–21 January, 3–18 February, 24–31 March, 2–8 and 25–28 April 2012,. In the 2010–11 breeding season, nest boxes were observed between 20:00 and 03:00 to record the arrival and departure time of the parent birds. All nests were set with a one-way gate to allow the capture of parent birds for identification and to measure their body mass after feeding their chicks (see Chapter 2 or Kim et al. 2014 for details of trap setting). In 2011–12, 20 nest boxes were monitored in the same manner with the addition of 10 infrared cameras in front of 10 nests to monitor the nest attendance continuously throughout the breeding season. Each bird was banded with metal identification rings in past years, their sex determined and/or age and previous breeding experience available for some birds (O'Dwyer et al. 2006c). Where sex was unknown, feather samples were collected either at the beginning or end of the breeding season and sex determined by analysis of DNA using DNA solutionsTM.

In addition to trapping and infrared cameras, adult arrival at the nest was also confirmed by temperature loggers within geolocators. The use of temperature loggers to detect parental visits has been validated in Chapter 3. The time elapsed between two arrivals at the nest represented the duration of an individual trip in days. The visit was coded as unknown when the sex of the adults could not be identified.

5.3.3 CHICK GROWTH AND MEAL SIZE

Chicks were weighed to the nearest gram with a 300-g Pesola spring scale or, if chicks exceeded 300 g, to the nearest 5 g with a 500-g Pesola scale. Mass changes in the six hours between 1200 and 1800 were used to calculate mass loss due to respiration and defecation.

Meal size was calculated by adding the predicted mass loss over 18 hours to any overnight mass increase.

Feeding frequency was calculated by using the method of Ricklefs et al. (1985). If (1) proportion p of parents fed their chick each night and proportion $q = 1 - p$ did not, and (2) if parents fed their chicks independently of each other, then proportion q^2 of chicks would not be fed, proportion $2pq$ would be fed by one parent or the other, and proportion p^2 would be fed by both.

Meal size was compared among years and sex with generalized linear models including year and sex as a fixed effect and the nest ID as random term mass measurement nested within each nest to control for pseudo replication, because in many cases more than one mass change per individual chick was recorded. Relationship between the duration of foraging trips and adult body mass on return and meal size was tested by Pearson Correlation. If the test result shows $P \geq 0.05$ but r^2 value is relatively high, observed statistical power was calculated in <http://www.danielsoper.com/statcalc3/default.aspx>.

5.3.4 DIET SAMPLING

Diet samples were collected 7–8 February, 4–5 March and 9–10 April in 2011, and 4–5 February and 27 March – 4 April in 2012. Adult Gould's Petrel were caught on their return to the nest, and water flushing (Gales 1987) was used to induce regurgitation of stomach contents, prior to chick feeding. This technique involves forcing warm water into the proventriculus through a plastic tube and, once regurgitation begins, inverting the bird to ease the process. Although it is possible that the stomach may not be completely emptied (Lishman 1985, Jackson & Ryan 1986), water flushing is regarded as simple, easy and less harmful than other stomach pumping techniques (Duffy & Jackson 1986). Flushing was generally

performed once on each bird with a second attempted if no hard parts were recovered from the first flush. Adult birds, intercepted while returning from provisioning trips, sometimes regurgitated spontaneously when being handled. These regurgitants were collected without employing water flushing. After flushing or collection of material from handling, red plastic rings were attached to the tarsus of the adults, ensuring one sample per year to minimise disruption of feeding frequency to their chick. The same flushing technique was used to collect diet samples from chicks. Body mass data were also collected so that a meal of thawed squid and white bait could then be hand fed to the chick to replace the lost meal. Various numbers of samples were collected each month (Table 5.3). In April, during the fledging period, adult visits were rarely intercepted so no targeted samples were collected except from a single adult intercepted in April 2012. In 2012, further collection of stomach contents was planned for March, but high seas prevented access to the island. I did not collect samples in April 2012 as stomach contents from near-fledged birds at this time in 2011 barely contained any hard part remains. Due to the small number of samples in 2012, only 2011 samples were statistically tested to compare between months.

Each collected sample had excess water and oil removed after a short settling period, then 99% ethanol was added to slow further degradation of the sample. Most samples were transported to the mainland for refrigeration within a day, however, where this was not possible, samples were filtered to collect hard parts such as otoliths, bones, cephalopod beaks, eye lenses and exoskeletons. These hard parts were stored at room temperature until transported to the laboratory.

Examination and identification of samples began with sorting to retrieve hard remains. These materials were washed and stored in new 99% ethanol and sagittal otoliths and cephalopod

lower beaks were taken for microscopic imaging. Otolith identification protocols followed those set out in Furlani et al. (2007). Only cephalopod lower beaks were used for identification because the lower beak shows far greater morphological variation between species (Xavier et al. 2011). The lower cephalopod beak identification followed features and keys from Clarke (1986) and Xavier and Cherel (2009).

5.4 RESULTS

5.4.1 FORAGING LOCATIONS AND AREAS

In 2011, as mentioned in Materials and methods, data were live-downloaded whenever tagged birds were intercepted and at-sea locational data collected from 29 individuals (15 males, 11 females, 3 unknown sex) from 18 nests were available to be analysed. In 2012, of the 40 individuals carrying tags, 34 tags were retrieved and data were successfully downloaded from 15. Data from two loggers were discarded as they constantly showed unrealistic locations (e.g. in the Arctic or no existing coordinates), therefore only thirteen birds (5 males, 7 females, 1 unknown sex) from ten nests were included in the analyses. Among these birds, seven (3 males and 4 females) in five nests were tracked for two years.

During incubation, Gould's Petrels undertake long foraging trips lasting 10–15 days on average while the fasting partner incubates (Chapter 4). The kernel density analysis showed that partners of incubating birds foraged mainly east of Tasmania during 2011 and 2012 (Figure 5.1 A and C). While the movement of five males and three females in 2011 were concentrated in the waters around Tasmania (Figure 5.1 A), movements of two males extended east of Tasmania and towards New Zealand in 2012 (Figure 5.1 C). Females

conducted more extended trips to the west of Tasmania, while males tended to stay east of Tasmania or in South Australian waters (Figure 5.2).

Following hatching, both parents foraged extensively in waters close to the colony and the shelf edge (Figure 5.1 B and D, and Figure 5.2) so they could regularly return to the nest. Although males in 2012 tended to feed closer to the mainland than males in 2011, there was high overlap in locations foraged. While birds exclusively foraged in the western Tasman Sea during incubation periods, occasionally birds used the Coral Sea and waters around New Zealand, as well as the Tasman Sea, during chick rearing periods (Figure 5.2).

Although core foraging areas (<50% UD) were similar, there were annual and monthly differences in the broader distribution (75% and 95%, respectively Table 5.1 and Figure 5.2). In January and February 2011, adult Gould's Petrel foraged predominantly in the Tasman Sea and in the waters to the south of eastern Australia. In March 2011, adults were more widely distributed, extending far to both the north and south of Australia. In 2012, birds also foraged further east in waters around New Zealand and New Caledonia.

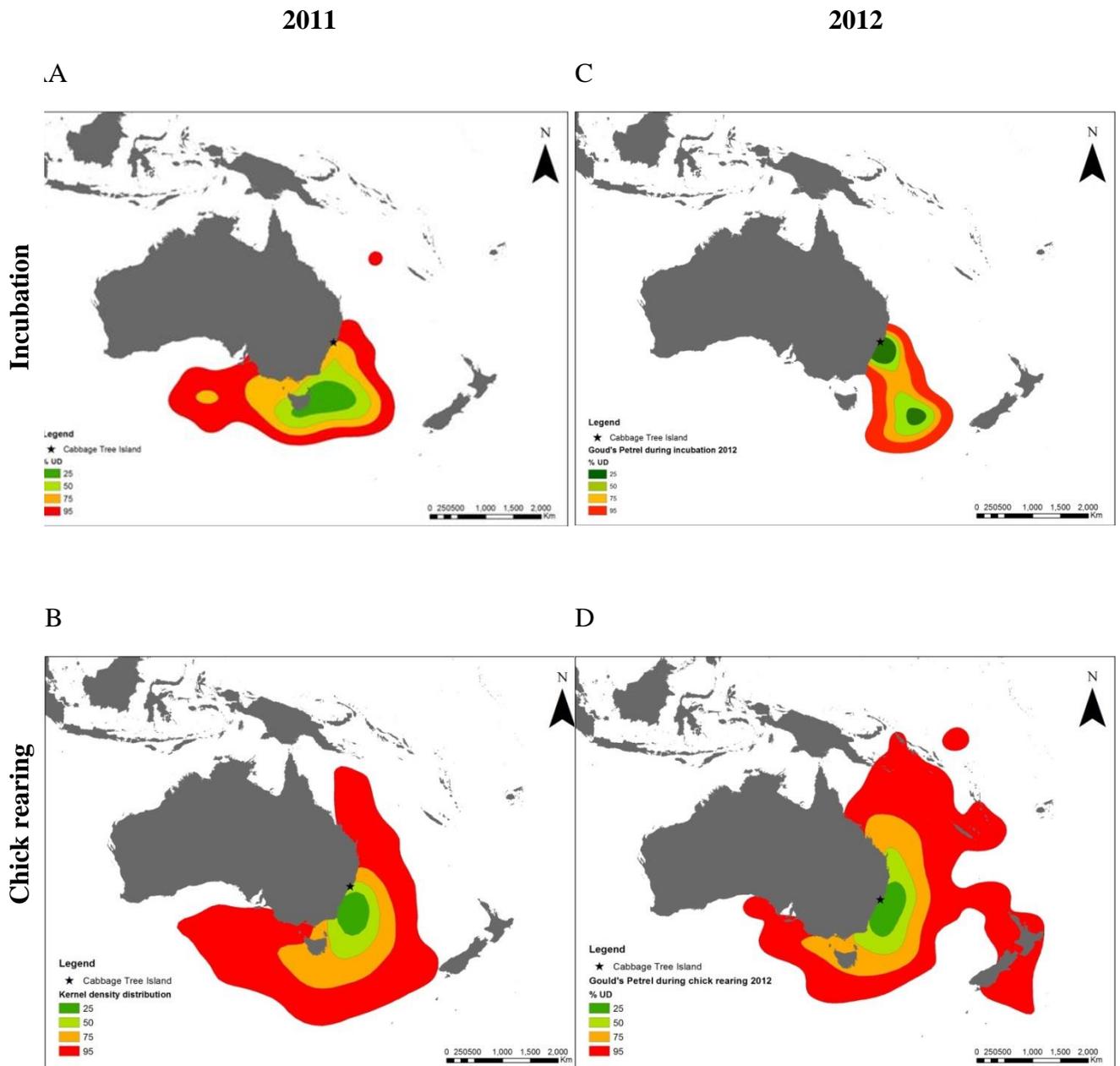


Figure 5.1 Kernel density distribution of Gould's Petrel during incubation and chick rearing in 2011 and 2012.

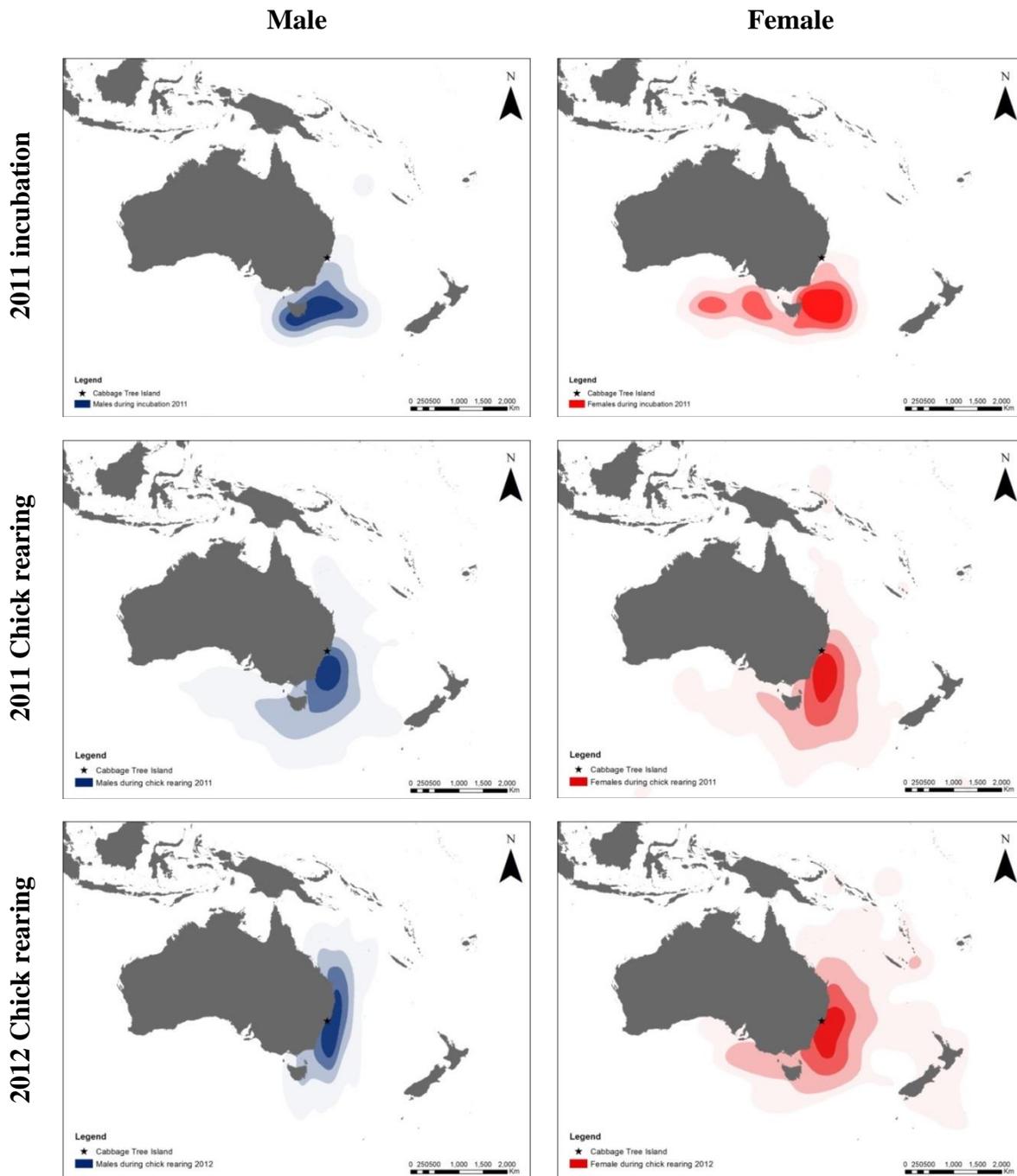


Figure 5.2 Kernel density distributions (95%, 75%, 50% and 25%) of foraging zones used by males (blue) and females (red) of Gould's Petrel at different stages of breeding in 2011 and 2012.

Kernel density maps of January, February and March in 2011 and 2012 were overlaid on SST (Figure 5.3), Chl *a* concentration (Figure 5.5) and bathymetry (Figure 5.7). Generally, birds foraged in areas where SST was between 10–30°C in both years (Figure 5.4) and birds in 2011 were present in colder water than birds in 2012 (Table 5.1). During long foraging trips in January and February, birds tended to go to cold waters in 2011, while birds travelled to both cold and warm waters in the tropics in 2012 (Figure 5.3). In general, birds foraged in waters where Chl *a* concentration was between 0.05–0.40 (Figure 5.6), and in 2011 used more productive waters than birds in 2012 (Table 5.1). There was no strong relationship between foraging distribution and Chl *a* concentration, although Figure 5.5 shows that long foraging trips to waters south-east of Tasmania and close to New Zealand were loosely associated with high concentrations of Chl *a*. Gould’s Petrels predominantly used waters between 4000 and 5000 m deep (Figure 5.7 B). Frequency distribution of bathymetry encountered by tagged birds shows consistent use of deep waters throughout the breeding season (Figure 5.8).

Table 5.1 Intra- and inter-year differences in spatial environmental variables of core foraging areas of Gould's Petrel. Range is presented in brackets.

| Month | Variables | 2011 | 2012 | Mann-Whitney U | P |
|----------|-----------------------------------|---------------------------------|---------------------------------|----------------|--------|
| January | SST (°C) | 20.87 ± 2.38 (15.52 – 25.04) | 21.86 ± 2.70 (16.47 – 27.20) | 877083 | <0.001 |
| | Chl <i>a</i> (mg/m ³) | 0.17 ± 0.10 (0.05 – 0.98) | 0.13 ± 0.11 (0.03 – 0.96) | 379891 | <0.001 |
| | Depth (m) | -4179 ± 1201 (-5867 – -2) | -3308 ± 1942 (-5434 – -1) | 886256 | <0.001 |
| February | SST (°C) | 21.57 ± 2.93 (15.22 – 25.71) | 23.78 ± 2.00 (19.44 – 27.06) | 1061023 | <0.001 |
| | Chl <i>a</i> (mg/m ³) | 0.15 ± 0.08 (0.04 – 0.93) | 0.11 ± 0.10 (0.04 – 0.99) | 340507 | <0.001 |
| | Depth (m) | -4184 ± 1195 (-5671 – -3) | -3938 ± 1472 (-1 – -5380) | 779667 | 0.30 |
| March | SST (°C) | 19.58 ± 3.66 (12.86 – 25.42) | 21.79 ± 2.19 (17.21 – 25.19) | 1091726 | <0.001 |
| | Chl <i>a</i> (mg/m ³) | 0.22 ± 0.11 (0.06 – 1.00) | 0.15 ± 0.09 (0.05 – 1.00) | 459323 | <0.001 |
| | Depth (m) | -4033 ± 1275 (-5865 – -6) | -4111 ± 1299 (-5617 – -1) | 753990 | <0.001 |

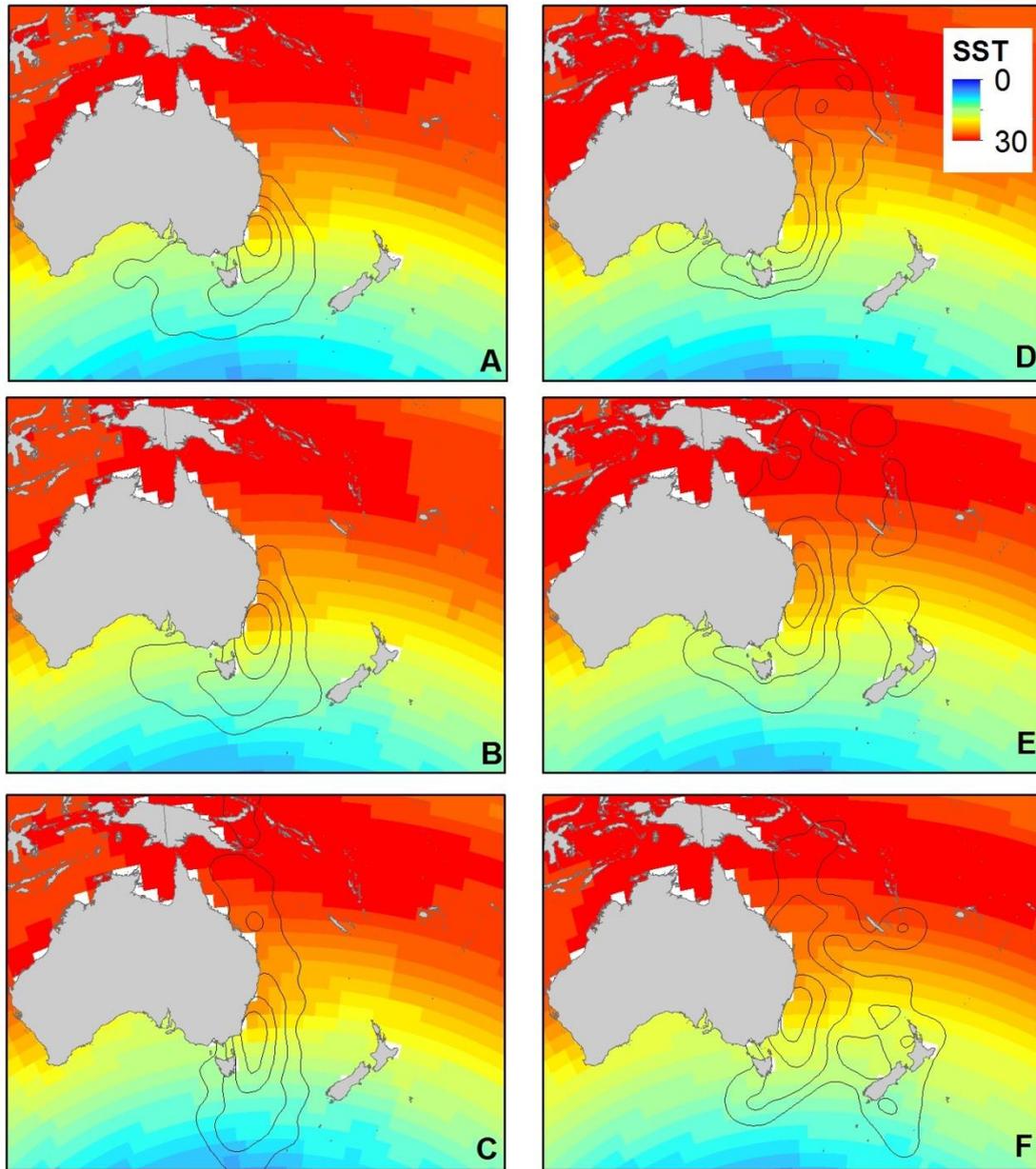


Figure 5.3 Kernel density distribution for Gould's Petrel during the chick rearing period overlaid on sea surface temperature; (A) January 2011, (B) February 2011, (C) March 2011, (D) January 2012, (E) February 2012, (F) March 2012.

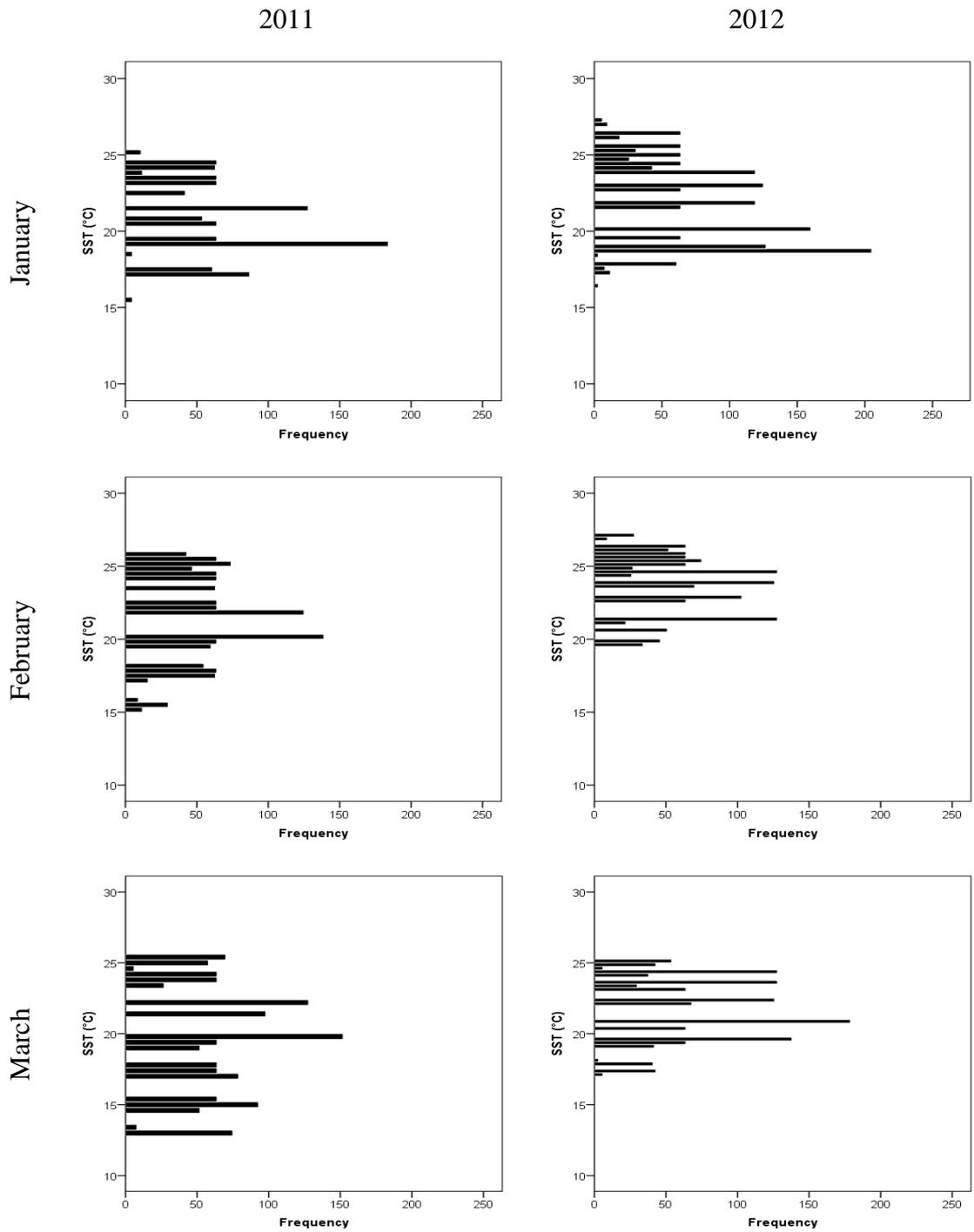


Figure 5.4 Frequency distribution of sea surface temperature encountered by Gould's Petrel during January, February and March in 2011 and 2012.

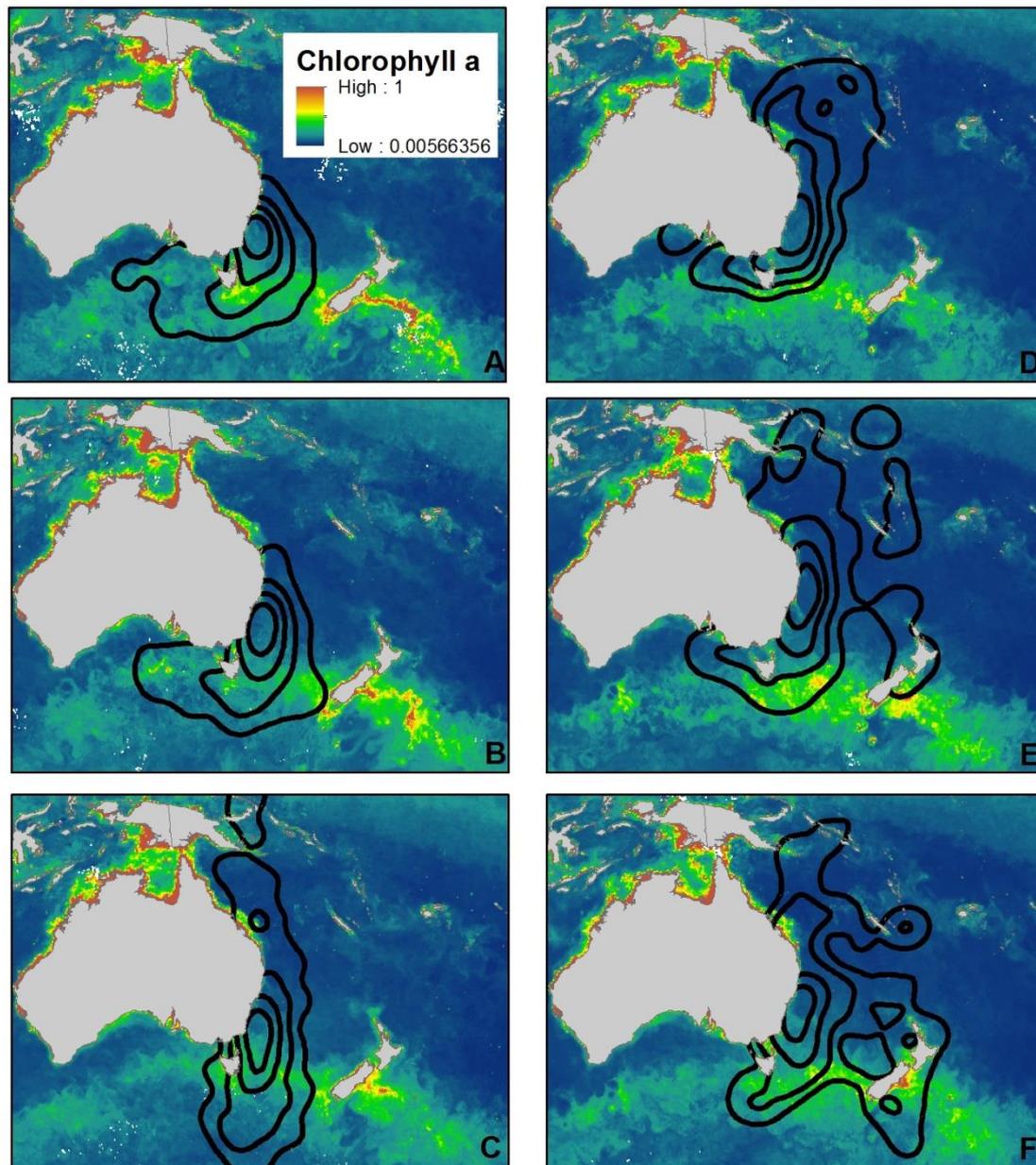


Figure 5.5 Kernel density distribution of Gould's Petrel during chick rearing overlaid on Chlorophyll *a* concentration; (A) January 2011, (B) February 2011, (C) March 2011, (D) January 2012, (E) February 2012, (F) March 2012.

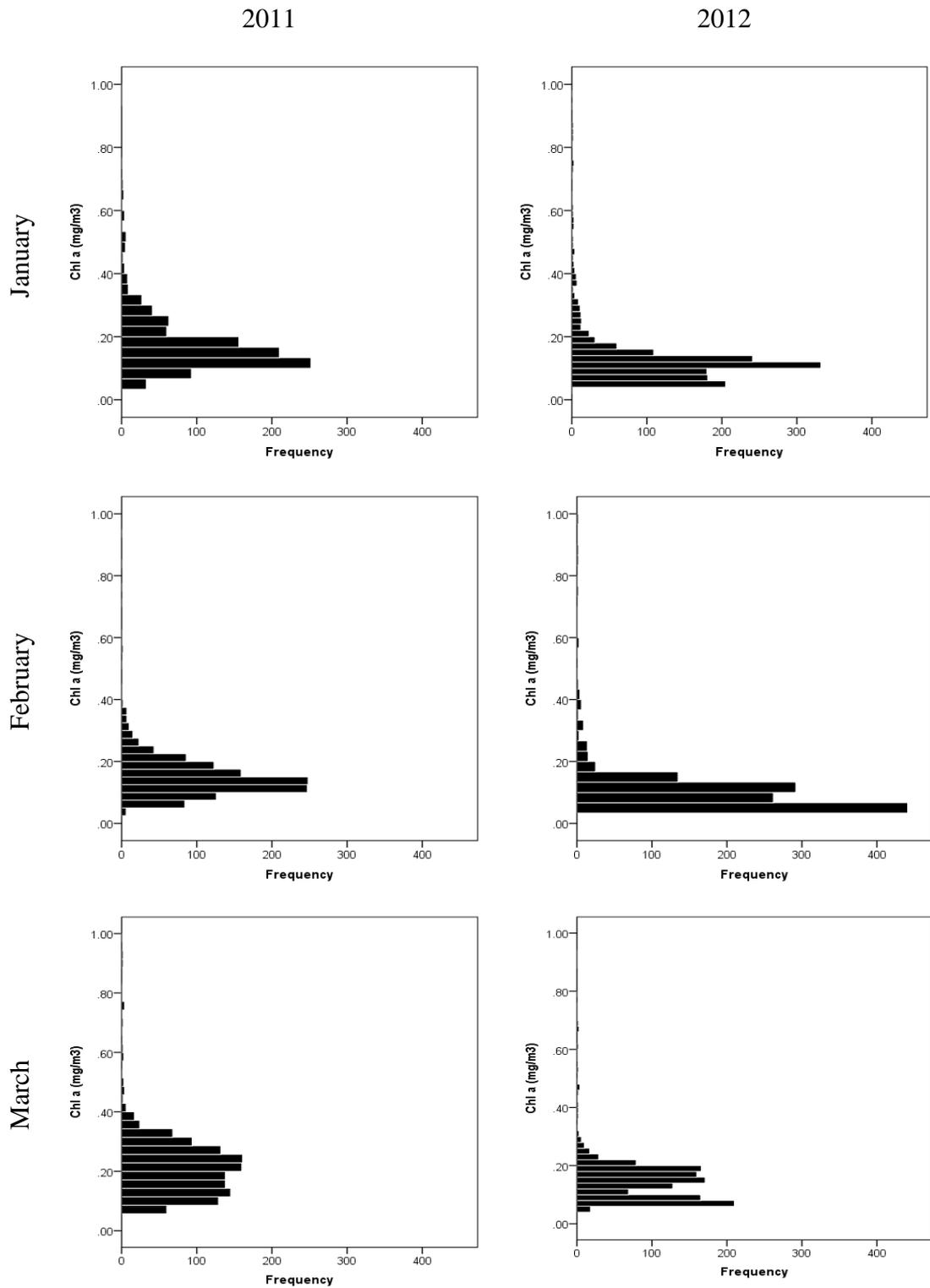
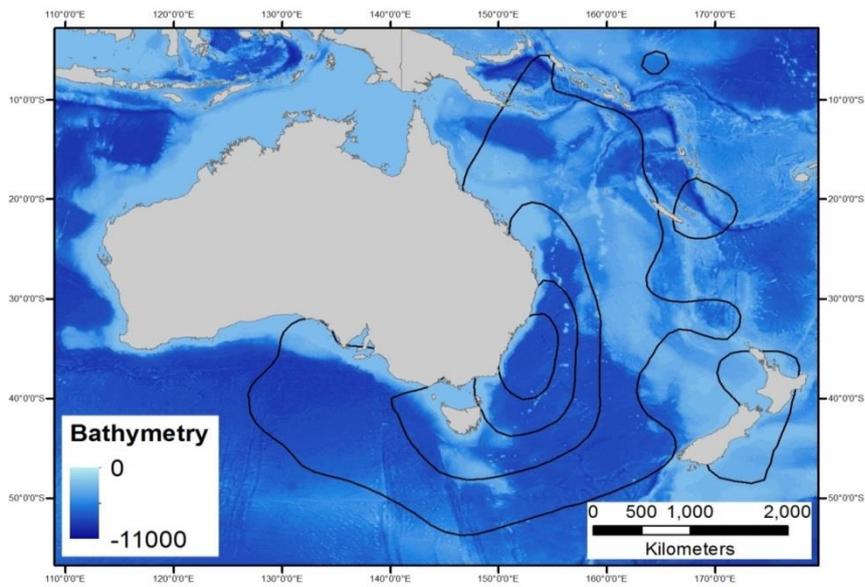
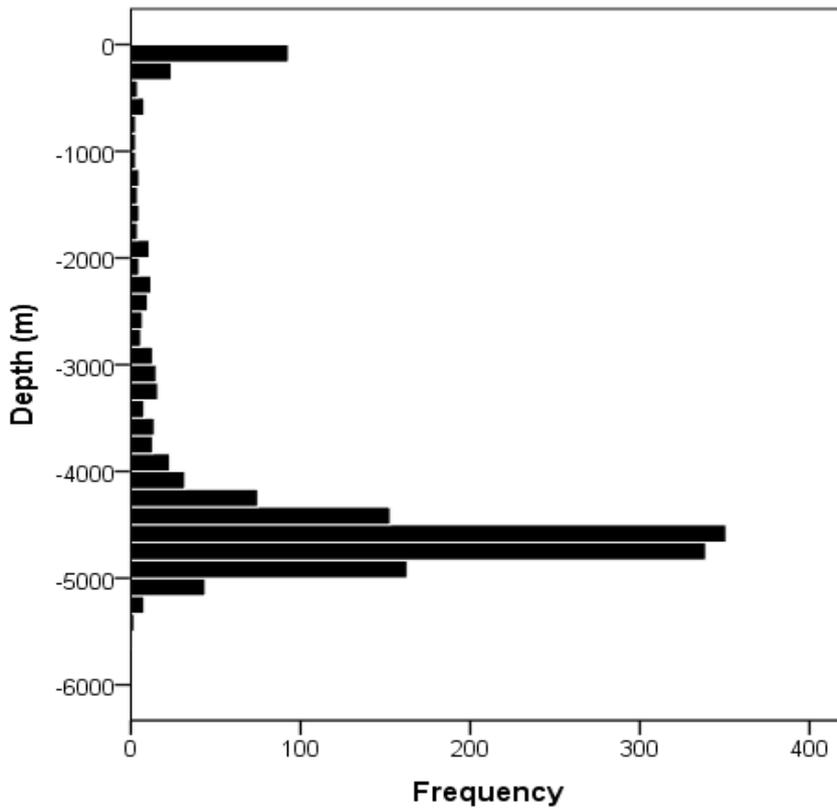


Figure 5.6 Frequency distribution of Chlorophyll *a* concentration encountered by Gould's Petrel during January, February and March in 2011 and 2012.



A



B

Figure 5.7 Kernel density distribution of Gould's Petrel during the breeding season in 2011 and 2012 (A) overlaid on bathymetric contours and (B) frequency distribution of bathymetry encountered by 50% kernel density distribution.

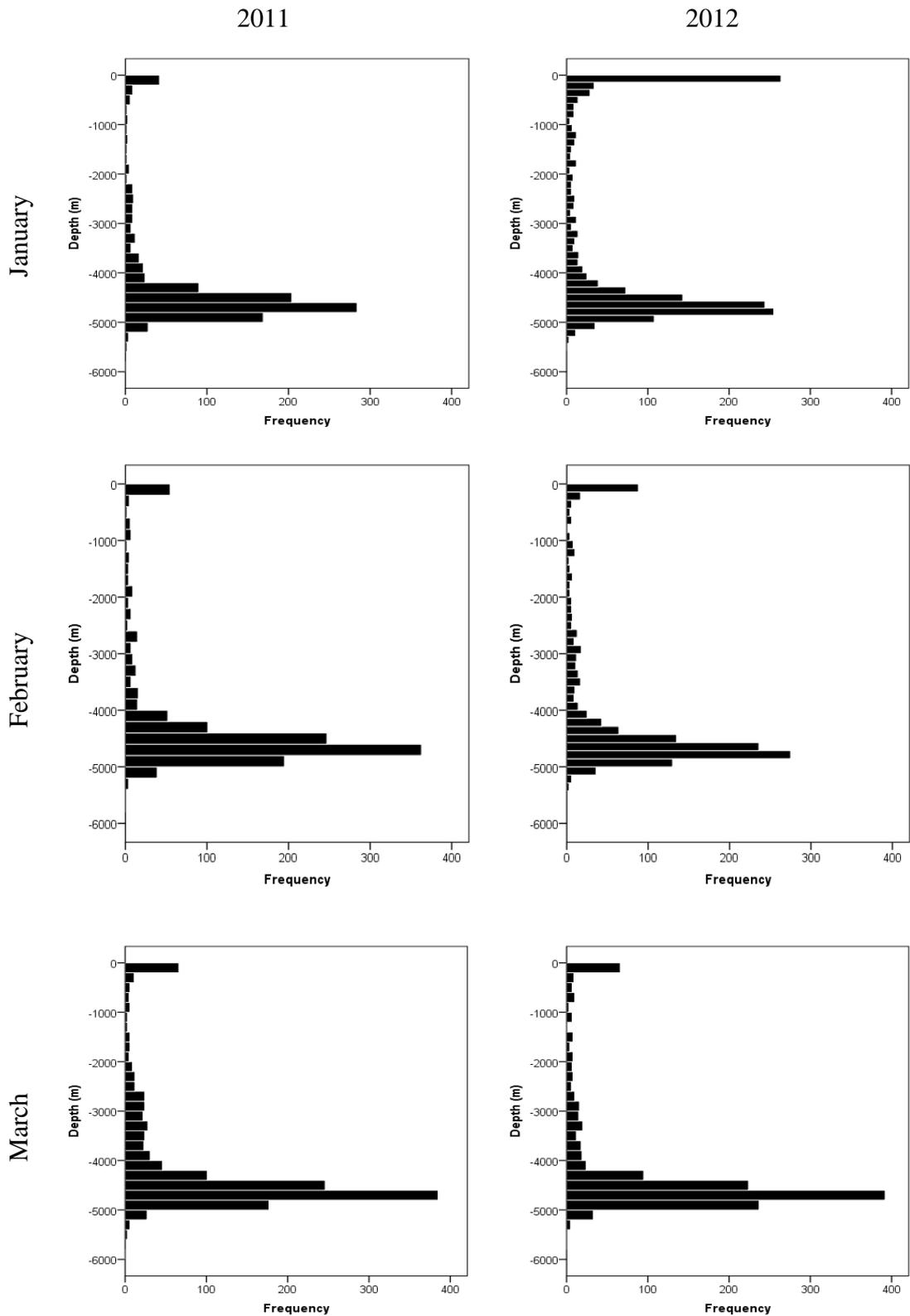


Figure 5.8 Frequency distribution of bathymetry encountered by Gould's Petrel during January, February and March in 2011 and 2012.

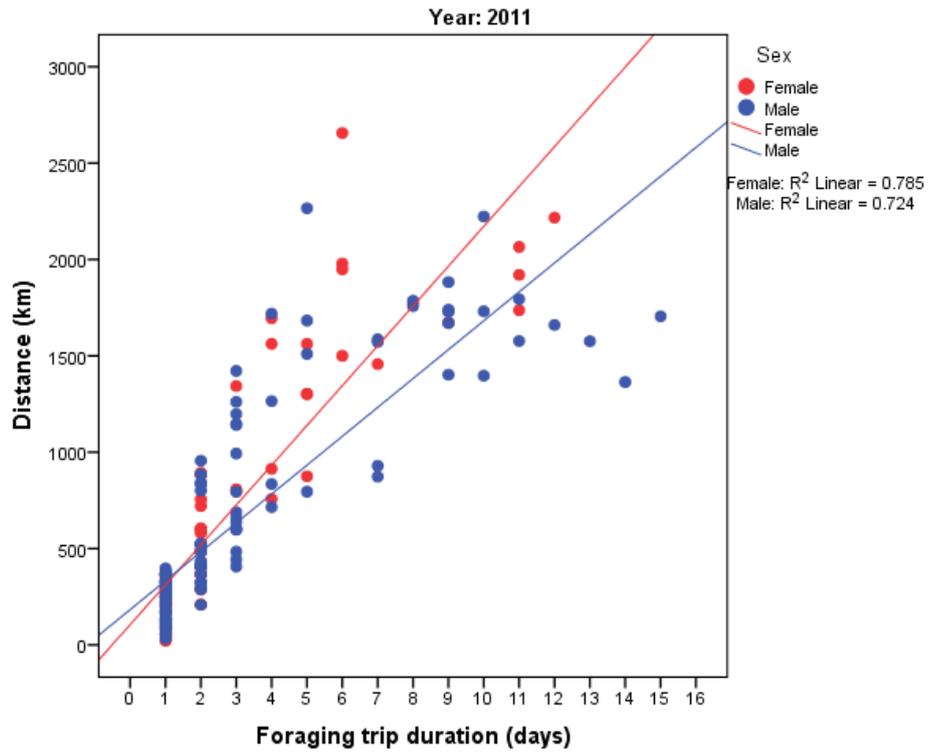
A proximity analysis using location data found that the mean distance from the colony during the chick provisioning period was 635 ± 563 km, and greater distances were travelled when birds foraged for longer (Linear regression, $F = 434.219$, $df = 1$, $P < 0.001$, Figure 5.9 and Table 5.2). Foraging distance from the colony showed a stronger relationship with foraging trip durations for both males ($y = 184 + 150x$, $r^2 = 0.724$, $P < 0.001$) and females ($y = 106 + 207x$, $r^2 = 0.785$, $P < 0.001$) in 2011 compared to 2012 (males: $y = 331 + 77.66x$, $r^2 = 0.416$, $P < 0.001$; females: $y = 771 + 43.47x$, $r^2 = 0.524$, $P < 0.001$).

The proportion of time spent on the water per day was $15.8 \text{ h} \pm 10.0\%$ ($n = 852$). Time spent on the water during daylight ($9.3 \text{ h} \pm 7.3\%$, range 0–43%) was significantly higher than during darkness ($6.6 \text{ h} \pm 5.8\%$, range 0–55.5 %) (paired t-test, $t = 9.6$, $df = 851$, $P < 0.001$).

Table 5.2. Trip duration (days) and mean distance travelled (km) in 2011 and 2012.

| Year | 2011 | | 2012 | |
|----------------------|-----------------|------------------------|-----------------|------------------------|
| Trip duration (days) | Number of trips | Mean distance \pm SE | Number of trips | Mean distance \pm SE |
| 1 | 106 | 232 ± 10 | 39 | 196 ± 15 |
| 2 | 34 | 526 ± 37 | 25 | 420 ± 48 |
| 3 | 19 | 843 ± 73 | 13 | 650 ± 111 |
| 4 | 8 | 1183 ± 151 | 11 | 830 ± 153 |
| 5 | 8 | 1411 ± 165 | 8 | 928 ± 123 |
| 6 | 4 | 2021 ± 238 | 3 | 1155 ± 527 |
| 7 | 5 | 1283 ± 158 | 2 | 1377 ± 207 |
| 8 | 3 | 1772 ± 8 | 1 | 473 |
| 9 | 6 | 1682 ± 64 | 3 | 748 ± 273 |
| 10 | 3 | 1783 ± 240 | 4 | 1202 ± 196 |
| 11 | 5 | 1818 ± 83 | 2 | 1118 ± 115 |
| 12 | 2 | 1938 ± 279 | 4 | 1639 ± 349 |
| 13 | 1 | 1575 | 3 | 901 ± 121 |
| 14 | 1 | 1364 | 4 | 1312 ± 130 |
| 15 | 1 | 1705 | 1 | 1319 |
| 16 | 0 | N/A | 2 | 1397 ± 149 |
| Total | 206 | 642 ± 592 | 125 | 622 ± 513 |

A



B

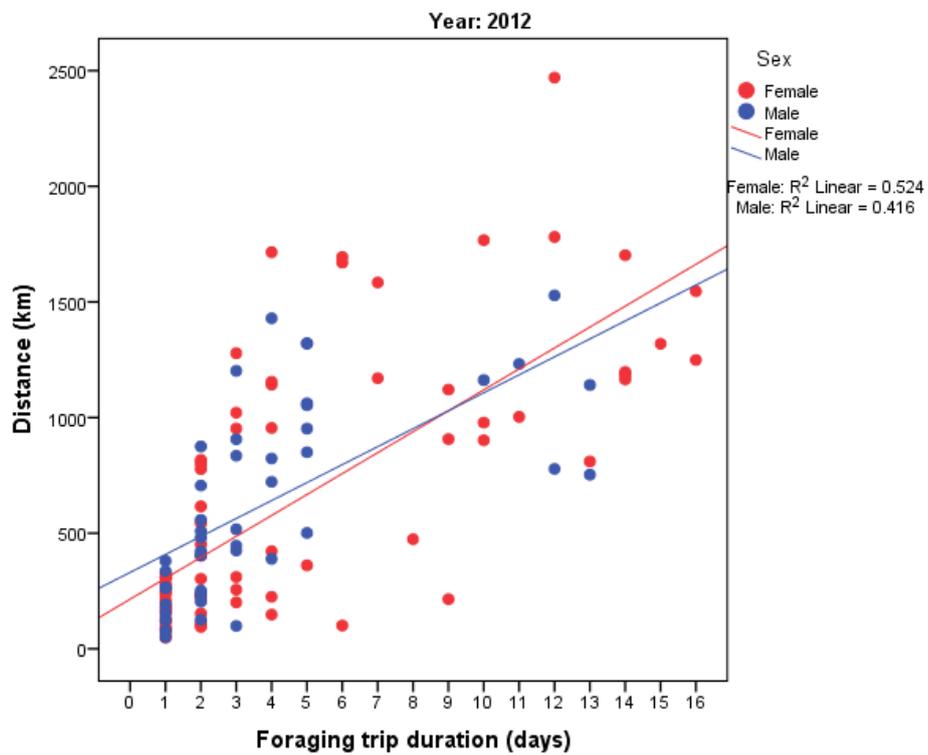


Figure 5.9 The relationship between foraging trip duration and distance from colony (km) by males and females of Gould's Petrels during chick rearing periods in (A) 2011 and (B) 2012.

5.4.2 NEST ATTENDANCE AND TRIP DURATION

Figure 5.10 shows the pattern of parental visits at 10 nests that were monitored by cameras. Although there was no clear dichotomy or pattern between short trip and long trip cycles, adults spent approximately half of their foraging time on longer trips (6 - 16 days).

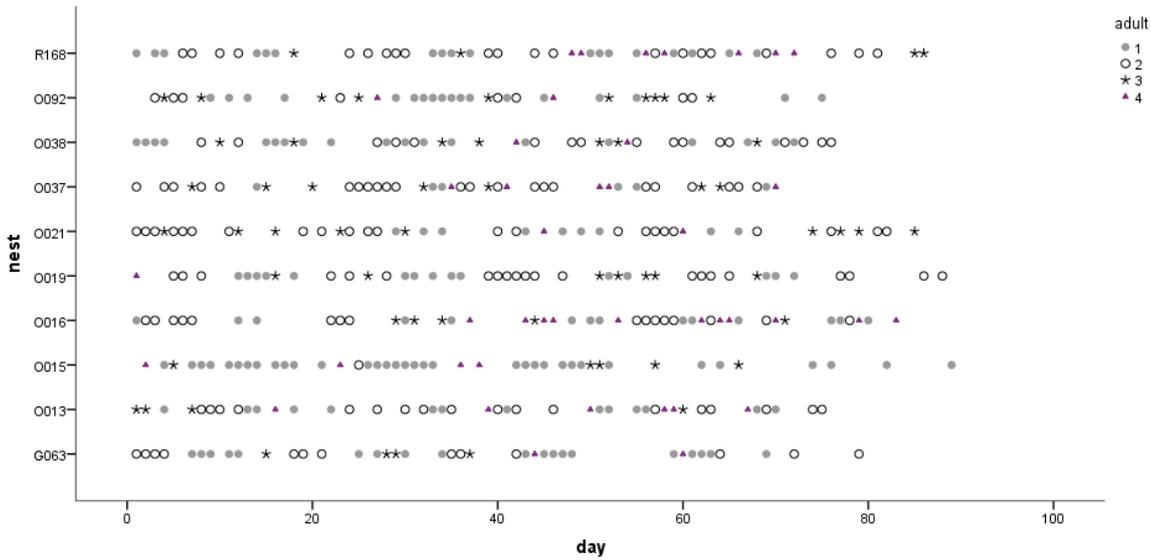


Figure 5.10 Feeding frequency of Gould's Petrel in 2012 (●: males, ○: females, *: bird not identified, ▲: double feeding).

Overall, foraging trip duration and frequency distribution patterns were similar between years (Figure 5.11). Both a Poisson (2011: Kolmogorov-Smirnov $Z = 4.04$, $p < 0.001$, $n = 237$; 2012: Kolmogorov-Smirnov $Z = 6.04$, $P < 0.001$, $n = 476$) and Normal distribution (Kolmogorov-Smirnov $Z = 4.94$, $p < 0.000$, $n = 237$; 2012: Kolmogorov-Smirnov $Z = 6.56$, $p < 0.001$, $n = 444$) showed that significantly more short trips of one or two day's duration were conducted than longer trips exceeding five days in both years (Figure 5.11).

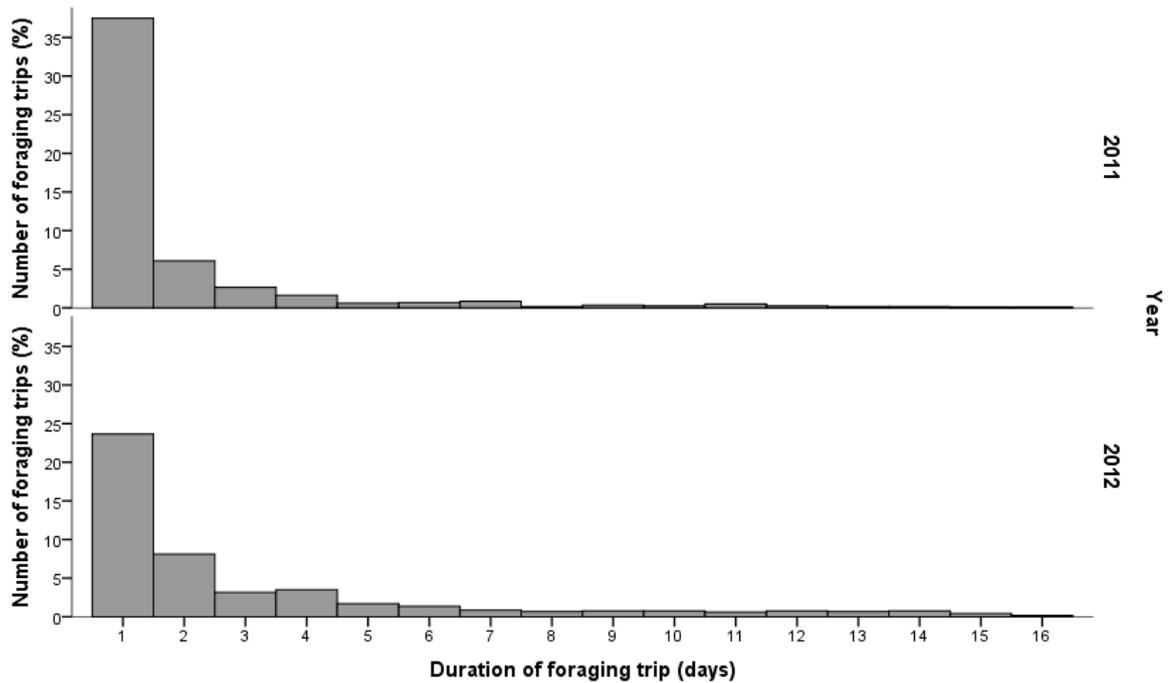


Figure 5.11 Distribution of foraging trip durations of Gould’s Petrel in 2011(upper) and 2012 (lower).

5.4.3 CHICK GROWTH AND MEAL SIZE

The mass of chicks averaged over each age (days before fledging, dbf) are presented in Figure 5.12. The growth curves are typical of Procellariiformes. During the early chick provisioning period (for Gould’s Petrel, 70–100 days before fledging) chick mass increased rapidly, followed by a period (30–40 days) of slower increases, followed by a period (~30 days) of mass decline. Average mass peaked approximately one month before fledging. During the middle of the chick provisioning period, mass fluctuated widely. Although statistically not tested due to small sample size, generally, the average chick mass from each period in 2011 was higher than the average of chicks in 2012. This difference was particularly evident in the central 40-day period. The steeper rate of mass gain during the 30–70 dbf period suggests that chicks in 2011 were fed a greater quantity of food than in 2012 or the food was of greater nutritional value.

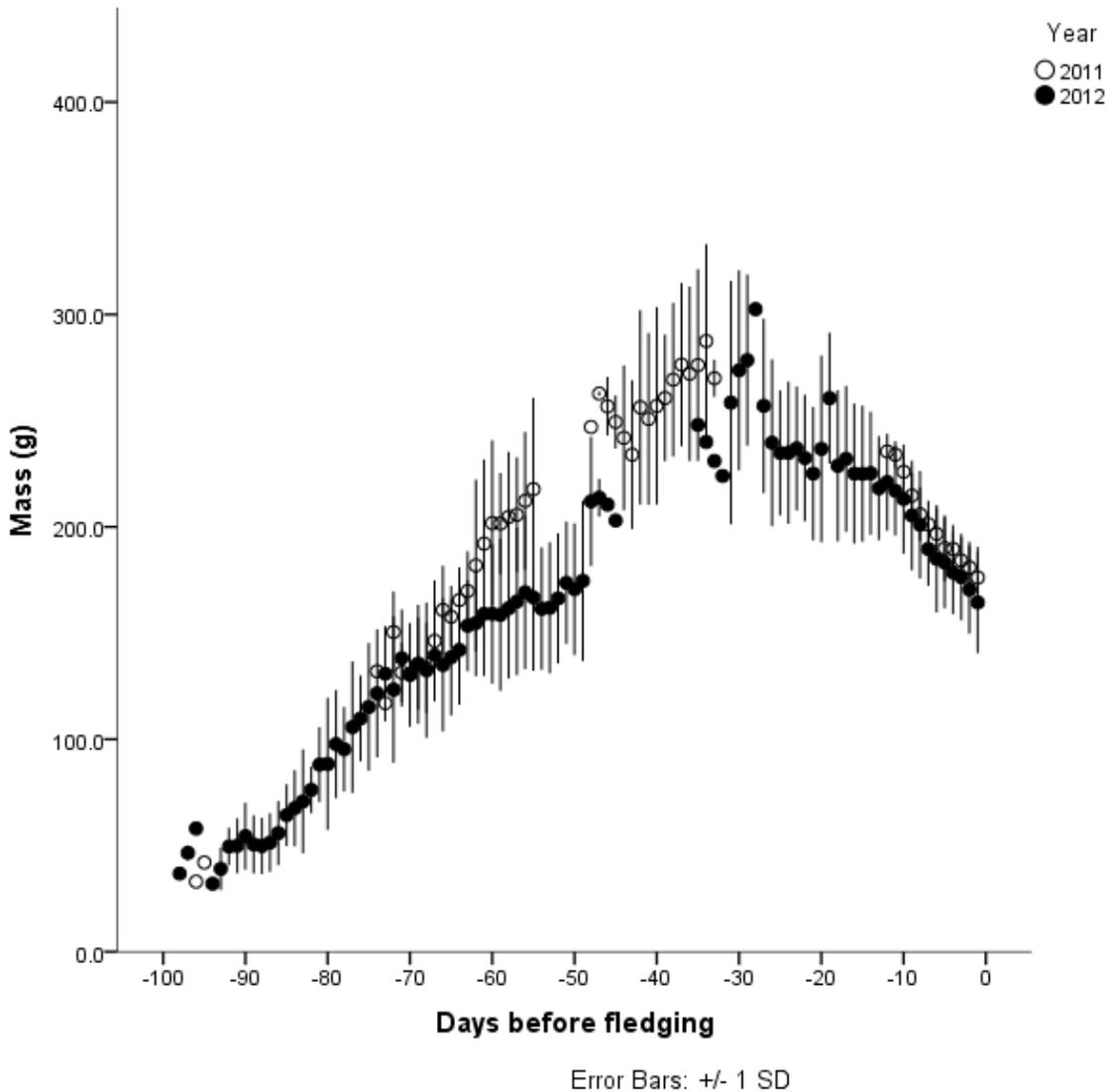


Figure 5.12: Average mass of Gould's Petrel chicks according to age.

In 2011, 50 chicks were weighed approximately 13 times each (range 1–24) representing 658 chick nights. In 2012, 23 chicks were weighed approximately 27 times each (range 2–35) representing 567 chick nights. When there was an overnight increase (i.e., the chick was fed), the chicks mass loss was 0.65 ± 0.03 (SE) g hours^{-1} ($n = 424$). When there was no increase, the mass loss was 0.53 ± 0.02 g hours^{-1} ($n = 547$), the two rates being significantly different ($t_{2,969} = -2.968$, $p = 0.003$). From these calculations, the probability that both parents fed their chick was calculated as 0.054 and 0.070 for 2011 and 2012, respectively. Therefore, 36 and

40 of the mass increments in 2011 and 2012, respectively, represented double feeds. Elimination of the double feeds from the calculations resulted in a mean meal size of 26.8 ± 7.9 g (range 11.6–42.6 g) in 2011 and 22.4 ± 6.6 g (range 11.6–34.6 g) in 2012, respectively. There was a significant difference in meal size between years (the likelihood ratio statistic = 11.977, $df = 4$, $p < 0.001$) and also a different pattern in the distribution of meal size between years (Figure 5.13). There was no difference in meal size delivered by male parents (27.8 ± 12.3 g in 2011 and 25.2 ± 9.4 g in 2012) and female parents (28.0 ± 10.5 in 2011 and 25.5 ± 9.1 g in 2012) (the likelihood ratio statistic = 0.373, $df = 4$, $p = 0.541$).

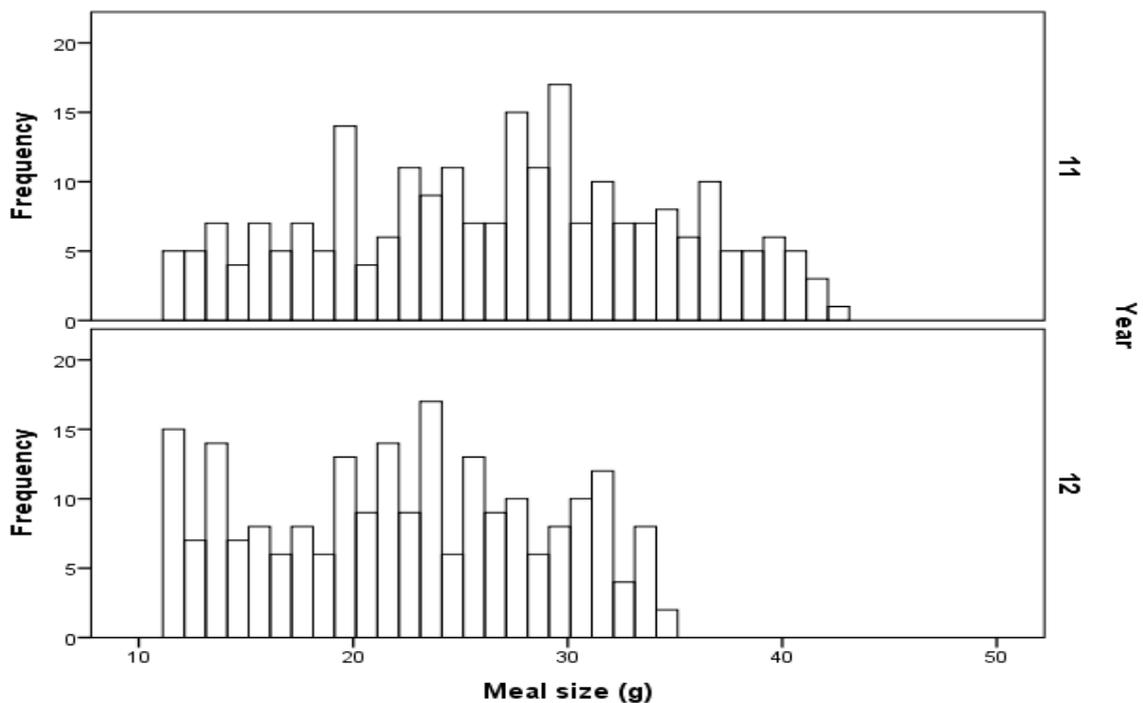
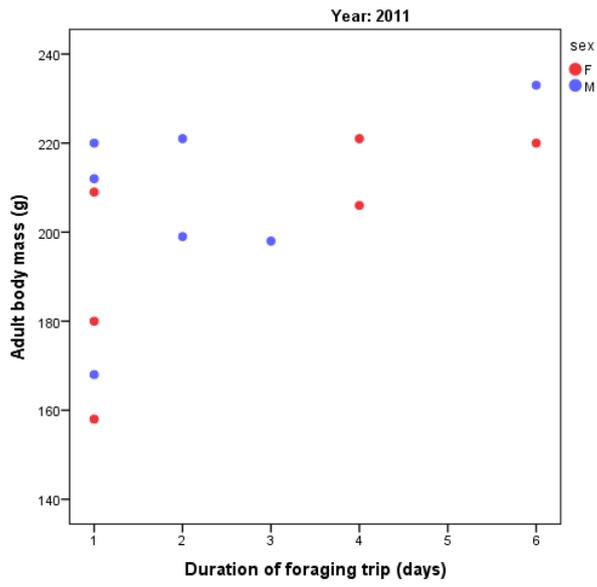


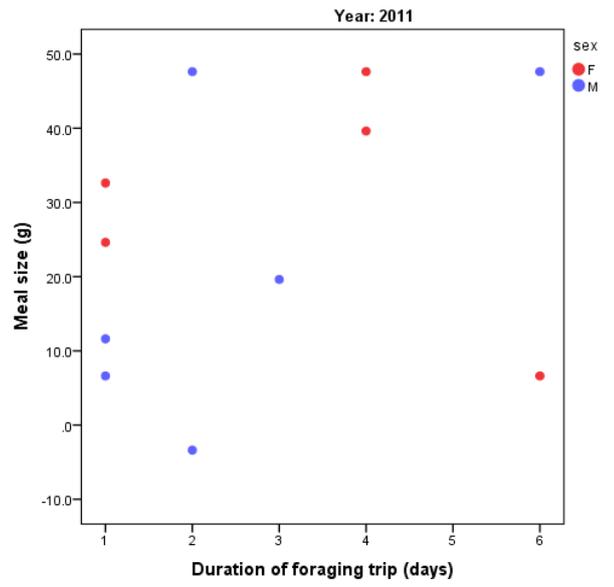
Figure 5.13 Frequency distribution of Gould's Petrel meal size in 2011 (upper) and in 2012 (lower).

In 2011, neither female nor male body mass on return were related to foraging trip duration (Female: Pearson Correlation, $r_6 = 0.720$, $P = 0.107$, $y = 175 + 8.41 x$, $r^2 = 0.518$, observed statistical power = 0.269; males: Pearson Correlation, $r_7 = 0.501$, $P = 0.251$, $y = 194 + 5.94 x$, $r^2 = 0.25$; Figure 5.14 A). In 2012, adult female body mass on return was very weakly

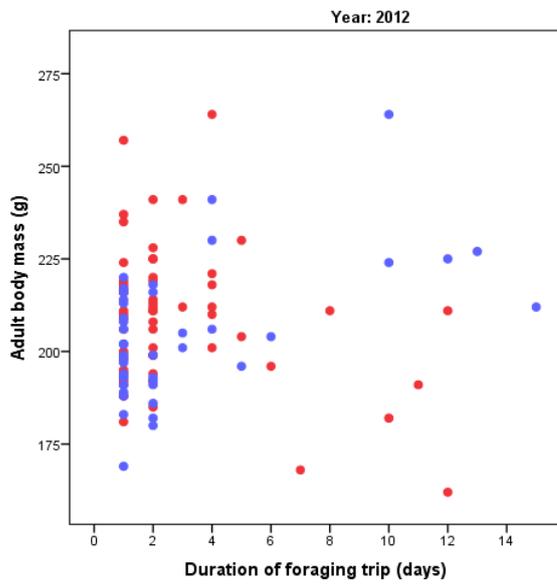
inversely related to foraging trip duration (Pearson Correlation, $r_{59} = -0.277$, $P = 0.034$, $y = 214 - 1.89x$, $r^2 = 0.077$; Figure 5.14 B), while male body mass was weakly positively related to foraging trip duration (Pearson Correlation, $r_{42} = 0.522$, $P < 0.001$, $y = 197 + 2.57x$, $r^2 = 0.273$; Figure 5.14 B). Meal size was not correlated to duration of foraging trip in 2011 (Female: Pearson Correlation, $r_6 = -0.276$, $P = 0.653$, $y = 36.62 - 2x$, $r^2 = 0.076$; Male: Pearson Correlation, $r_7 = 0.632$, $P = 0.178$, $y = 3.48 + 7.26x$, $r^2 = 0.400$; Figure 5.14 C). In 2012, there was a weak correlation between meal size delivered by males and duration of foraging trip (Pearson Correlation, $r_{42} = 0.503$, $P = 0.001$, $y = 28.55 + 0.05x$, $r^2 = 0.253$; Figure 5.14 D) but there was no relationship between meal size delivered by females and duration of foraging trip (Pearson Correlation, $r_{59} = 0.012$, $P = 0.926$, $y = 21.13 + 1.92x$, $r^2 < 0.001$; Figure 5.14 D).



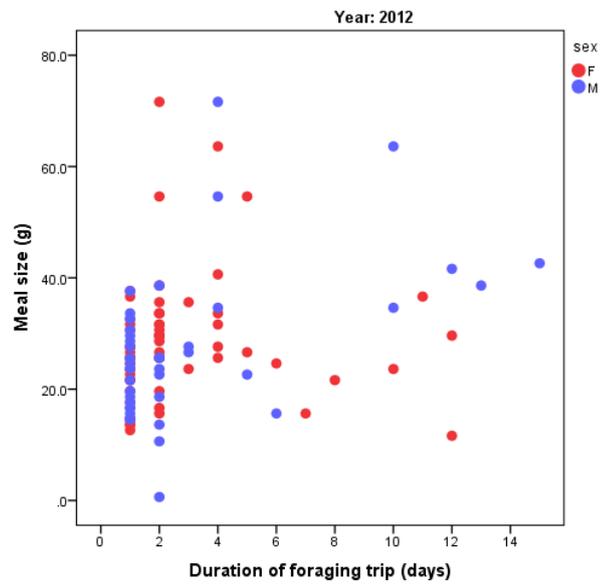
A



C



B



D

Figure 5.14 Relationship between the duration of foraging trips and adult body mass on return and meal size.

5.4.4 DIET

A total of 129 stomach samples were examined (Table 5.3). The identifiable parts belonged to either squid, fish or crustacean. Squid and fish were identified to species, genera or family (Table 5.4), however, crustaceans were not identified beyond subphylum (See Discussion). Other items present that could only be generally categorised included algae, worms and plastic.

Table 5.3 Stomach sample size collected from Gould's Petrel in Cabbage Tree Island during the breeding seasons.

| Month | | 2011 | 2012 | Sub Total | Total |
|-----------|-------|------|------|-----------|-------|
| February | Adult | 20 | 0 | 20 | 60 |
| | Chick | 16 | 24 | 40 | |
| March | Adult | 20 | 0 | 20 | 49 |
| | Chick | 22 | 7 | 29 | |
| April | Adult | 0 | 1 | 1 | 20 |
| | Chick | 19 | 0 | 19 | |
| Sub total | Adult | 40 | 1 | 41 | 129 |
| | Chick | 57 | 31 | 88 | |

Table 5.4 Diversity of cephalopod and fish remains from regurgitant of Gould's Petrels.

| Family | Genus | Species | Family | Genus | Species |
|-------------------------|-----------------------|--------------------|----------------------|--------------------|------------------|
| Cephalopod beaks | | | Fish otoliths | | |
| Architeuthidae | <i>Architeuthis</i> | | Tetraodontiformes | <i>Meuschenia</i> | <i>scaber</i> |
| Bathyteuthidae | <i>Bathyteuthis</i> | | Myctophidae | <i>Electrona</i> | <i>rissoi</i> |
| Cycloteuthidae | <i>Discoteuthis</i> | | | <i>Lampanyctus</i> | <i>australis</i> |
| Gonatidae | | | | | |
| Histioteuthidae | <i>Histioteuthis</i> | | | | |
| Lepidoteuthidae | <i>Lepidoteuthis</i> | | | | |
| Loliginidae | <i>Loligo</i> | <i>plei</i> | | | |
| | <i>Dorytheuthis</i> | <i>plei</i> | | | |
| Lycoteuthidae | | | | | |
| Mastigoteuthidae | <i>Mastigoteuthis</i> | | | | |
| Octopoteuthidae | | | | | |
| Sepiidae | <i>Sepia</i> | <i>officinalis</i> | | | |
| Sepiolidae | <i>Rossia</i> | | | | |
| Spirulidae | <i>Spirula</i> | <i>spirula</i> | | | |
| Chiroteuthidae | <i>Chiroteuthis</i> | | | | |

Squid was present in 62.9% and 59.4% of samples in 2011 and 2012 respectively, and there was no difference in frequency of occurrence of squid between years ($\chi^2 = 0.126$, $df = 1$, $P = 0.723$; Figure 5.15). Squid arms or mantle were present in 7 samples, 39 samples contained both upper and lower beaks and 34 samples contained either upper or lower beaks. Family Loliginidae dominated during both years. The frequency of occurrence of fish was more variable, with 56.7% and 37.5% in 2011 and 2012, respectively. However, the difference was not significant ($\chi^2 = 3.554$, $df = 1$, $P = 0.059$). Otolith identification showed *Electrona rissoi* was the dominant fish species consumed. During 2011 and 2012, crustaceans appeared in 25.8% and 40.6% of samples, respectively. There was no significant difference in the frequency of occurrence of crustaceans between years ($\chi^2 = 2.554$, $df = 1$, $P = 0.110$). The frequency of occurrence showed within year differences in 2011 (Figure 5.16) with the occurrence of fish significantly higher in both February and March, however, no fish were found in April ($\chi^2 = 31.021$, $df = 2$, $P < 0.001$). Percentage of occurrence of squid was consistently high from February to April ($\chi^2 = 4.919$, $df = 2$, $P = 0.085$), while occurrence of crustaceans peaked in March ($\chi^2 = 11.374$, $df = 2$, $P = 0.003$).

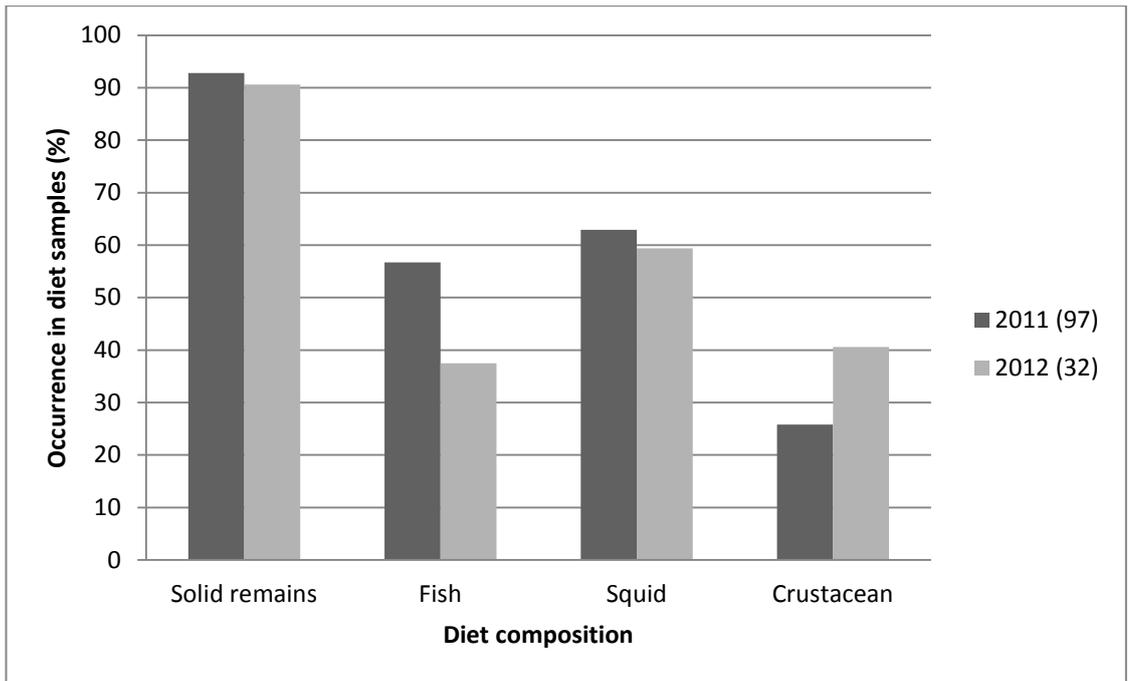


Figure 5.15 Diet composition of Gould's Petrel in two periods of chick provisioning in successive seasons.

Sample size in brackets.

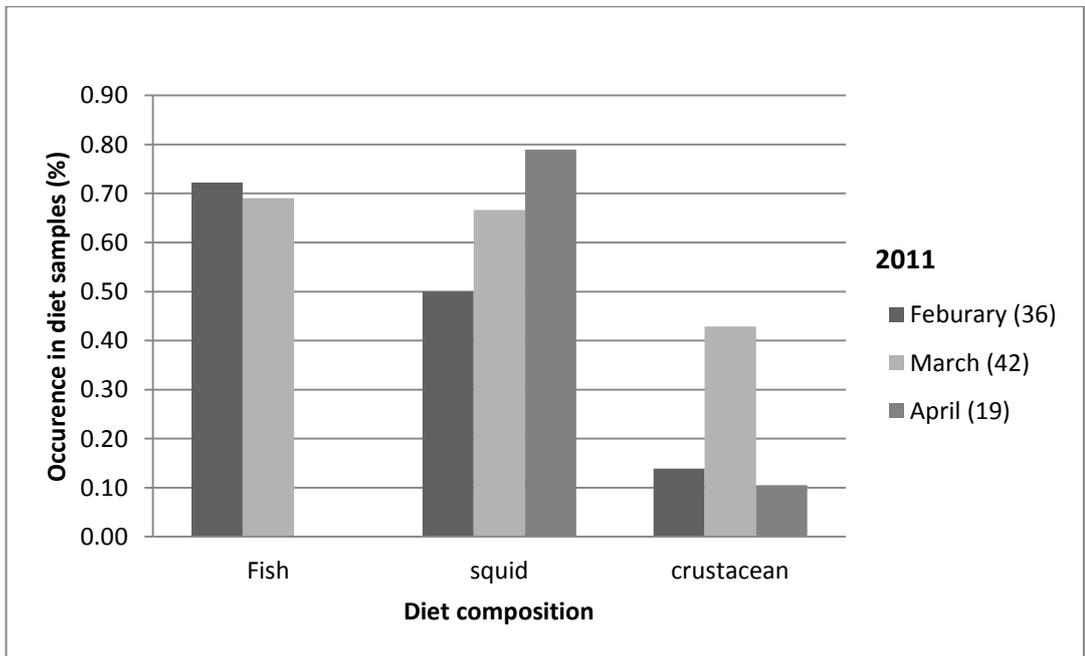


Figure 5.16 Diet composition of Gould's Petrels during three different chick provisioning periods in 2011; February (early chick provisioning), March (middle of the chick provisioning) and April (fledging period).

Sample size in brackets.

5.5 DISCUSSION

This chapter presents the first study to quantify the movements, at-sea distribution and activity patterns of Gould's Petrels during the breeding seasons. In 2011 and 2012, while the core foraging zones of Gould's Petrel were consistent between years, the areas exploited varied with different phases of the breeding cycle. During chick rearing adults foraged in waters close to the breeding colony presumably to meet the energy requirement of chicks. By contrast, to meet their own energy requirements they foraged in distant waters where it appears food was more readily available. Based on the patterns of nest visitation and the relationship between foraging trip duration and foraging locations, Gould's Petrel seem to adopt a dual foraging strategy during chick rearing.

5.5.1 FORAGING BEHAVIOUR

During the course of the breeding season, marked changes in foraging area were observed. During incubation periods where the core foraging area (50% UD) included waters to the east of Tasmania, chick rearing adults foraged closer to the breeding grounds on Cabbage Tree Island. Some other species utilise different foraging areas at different phases of the chick-rearing period. However, I did not observe temporal changes in the core foraging areas of Gould's Petrel during chick rearing, with data suggesting a preference for temperatures between 19 – 24 °C. There was no evidence that the at-sea distribution of breeding Gould's Petrel was influenced by SST beyond these upper and lower bounds, and only a weak relationship with Chl *a* concentration was found. This may be because, as central place foragers, movements of adults are constrained to returning to the colony by the energy needs of their chicks. To overcome this limitation, Gould's Petrel adopted dual foraging strategies. However, there was no clear separation between short and long trips as seen in other bird

species (Congdon et al. 2005). While many pelagic seabirds are thought to regulate effort by adopting a dual foraging strategy, a recent study has shown no evidence of dual foraging for four albatross species (Phalan et al. 2007). There is a possibility that environmental conditions determine whether seabirds adopt a dual foraging strategy or not; i.e., when food is readily available close to the breeding site, breeding adults might not need to take long trips to more distant and potentially more productive waters.

Bathymetry is known to affect the movement of birds (Yen et al. 2004). I found that Gould's Petrel used both shallow and deep waters, but occurred predominately over deep water (4–5 km deep). Like many other temperate and polar seabirds, Gould's Petrel probably rely on upwellings associated with oceanographic fronts, as well as shelf breaks and seamounts for feeding because these areas are more productive (Chapman et al. 2004). My tracking devices did not allow me to quantitatively analyse such relationships due to the high locational error (~184 km), however, if more accurate devices small enough to deploy on such small birds become available, further studies will be able to quantify the influence of biophysical factors on their movements. In addition to the biophysical factors I investigated, wind conditions are also known to affect the movement of birds either by shortening or by extending the time needed to return to the colony (Raymond et al. 2010) and are likely to also affect Gould's Petrel.

Differences between the sexes in foraging and food provisioning strategy have been found in bigger birds (Weimerskirch 1995, Weimerskirch et al. 1997, Welcker et al. 2009, Pinet et al. 2012). However, few studies have been carried out on small petrels and earlier work with other species did not indicate sex differences in adults during these behaviours (Rayner et al. 2007). During incubation, Gould's Petrel did not show sex differences in foraging behaviour

(Chapter 4), however, this conclusion was based on foraging duration only, and more studies using tracking technology were identified as a priority for future research. Although female Gould's Petrel tended to forage further west during the incubation period than males, very few individuals were tracked. Gould's Petrel did not show any sex differences in foraging locations and meal mass during chick rearing in 2011. However, in 2012 males tended to forage close to the east Australian coastline, whereas females ranged into oceanic waters of the Tasman Sea, closer to New Zealand. As shown in Figure 5.2, the distance females travelled from the colony during chick rearing was much further than the distance travelled by males. Generally masses of chicks were lower in 2012 than 2011 (Figure 5.12), sex differences in foraging strategy in 2012 might be due to poor condition in 2012. Other study (Gladbach et al. 2009) showed similar results, that males and females foraged in a similar way when good (high-krill) years but foraged differently during poor (low-krill) years. Foraging differently between sex is one way of risk partitioning, which leads to higher fitness at the pair level (Elliott et al. 2010).

5.5.2 PROVISIONING, MEAL SIZE AND CHICK GROWTH

Ricklefs (1992) calculated that intervals between successive feedings of the chick were about one third of the length of incubation spells. Gould's Petrel were expected to feed their chicks every 5 days considering the average incubation spell is 15 days (*see* Chapter 4). However, I found that feeding intervals were shorter than 5 days when chicks were very young, and increased toward fledging. Although Gould's Petrel chicks are known to be fed almost exclusively at night, some daytime feeding was confirmed by weight changes between 1200h and 1800h in the guard stage, when parents were present in the nest during daytime ($n = 2$). Newly hatched petrels receive small and frequent meals. For species that feed their chicks

frequently, as seen in Gould's Petrel, chance meetings of the two parents are more common (Figure 5.10). Considering inconsistency of trip durations, it is evidently only by chance that the parents return to the nest at the same time and provide double feeds. In some surface nesting tropical seabirds, nest visits without feeding the chick are common (Ricklefs 1984). Gould's Petrel is not a surface nesting species but visits without feeding did occur in this species ($n = 6$).

Because of the rapid loss of chick mass after feeding, overnight mass changes may not reveal small meals, and the sizes of large meals may be underestimated (Warham 1990). My calculation of mass loss for fed chicks (0.65 g hour^{-1}) was lower than in previous studies for fed chicks (0.97 g hour^{-1}), but mass loss for unfed chicks (0.53 g hour^{-1}) was higher (0.48 g hour^{-1}) (O'Dwyer 2004). The accuracy of measurement of meal size could have been improved by more frequent measurements of chick mass. However, this was intentionally avoided in this study in order to prevent the chick from being frequently disturbed. The problem of measuring meal size can be alleviated by weighing the adult before and after a meal. However, adults often regurgitate as a defence response when handled. Automatic weighing systems could be designed and installed at nest entrances to overcome these problems.

In 2011, adults performed more short trips and meal sizes were larger than in 2012. This might be because stomach contents are converted to a nutrient-rich oil when birds take long trips; or it might be that the birds took a long time to search for food when food availability was low. In 2011 the Chl *a* concentration in areas encountered by tagged birds was higher than in 2012, while SST was lower (Table 5.1). Accordingly, food availability is the more plausible explanation for annual differences especially as cold water is usually more

productive than warm water (Doney 2006), suggesting birds in 2011 were able to forage more efficiently. In addition, the average chick mass in 2011 was higher than the average chick mass in 2012 (Figure 5.12). This might be as a result of higher consumption of fish in 2011 compared to 2012. Fish has higher energy density of 5.61 KJ/g than squid with an energy density of 4.64 KJ/g.

5.5.3 FLEXIBILITY IN DIET

Cephalopod and fish identifications were based on the more common documented species, so the full range of prey items may not have been identified. Nonetheless, Gould's Petrel appears to have a diverse diet suggesting that they forage opportunistically and flexibly. There was a decline in fish in their diet in 2012 together with an increase in crustaceans (Figure 5.15) compared to 2011. Temporal variation also occurred within a single year (2011), with fish absent from the diet at the end of the breeding season, replaced by crustaceans (Figure 5.16).

Cephalopods were found to be the main prey type consumed by Gould's Petrel, suggesting that they are an important nutrient source for the species. The extent of dominance of cephalopods in the diet may have been overestimated because beaks persist for much longer in the stomachs of seabirds than do soft prey types such as copepods or other hard parts such as otoliths (Furness *et al.* 1984). Similarly, the importance of larger cephalopods may be overestimated because smaller beaks are digested more quickly (Imber 1973). Regardless, the most common squid beaks found in this study were from the Loliginidae family. All the species in this family live in shallow water over the continental shelves and come inshore to spawn (Cohen 1976 in Clarke (1986)). Even though the bathymetric maps showed that Gould's Petrel used both shallow and deep waters (Figure 5.7), it seems highly likely, given that cephalopods were a major prey item, that an important component of Gould's Petrel

foraging is in shallow coastal waters, a zone where environmental conditions are affected by rainfall. Increased rainfall can result in increased pollution, turbidity and reduced light penetration (Johnston & Gabric 2011), which in turn may potentially affect the spawning success of cephalopods and thus the dietary composition of Gould's Petrel.

The most common fish species of Gould's Petrel's diet was *Electrona rissoi*, a mesopelagic fish and one of the most abundant marine organisms, found predominantly on the continental slope (Catul et al. 2011). Based on the information that the subtropical convergence marks the southernmost limits of distribution of *E. rissoi* (Furlani et al. 2007), this species is assumed to be taken when Gould's Petrel foraged at Coral Sea. Most mesopelagic species make extensive upward migrations into the epipelagic zone during the night (Greely et al. 1999). As Gould's Petrels are not deep divers, these fish were most likely to be taken by the petrels at night, i.e. nocturnal foraging. Gould's Petrels have good night vision and olfactory capacity (Nevitt 2000) and can forage at night. Procellariiformes have the largest olfactory bulbs of any bird, suggesting that olfaction plays a fundamental role in searching for food, and in navigation or other activities.

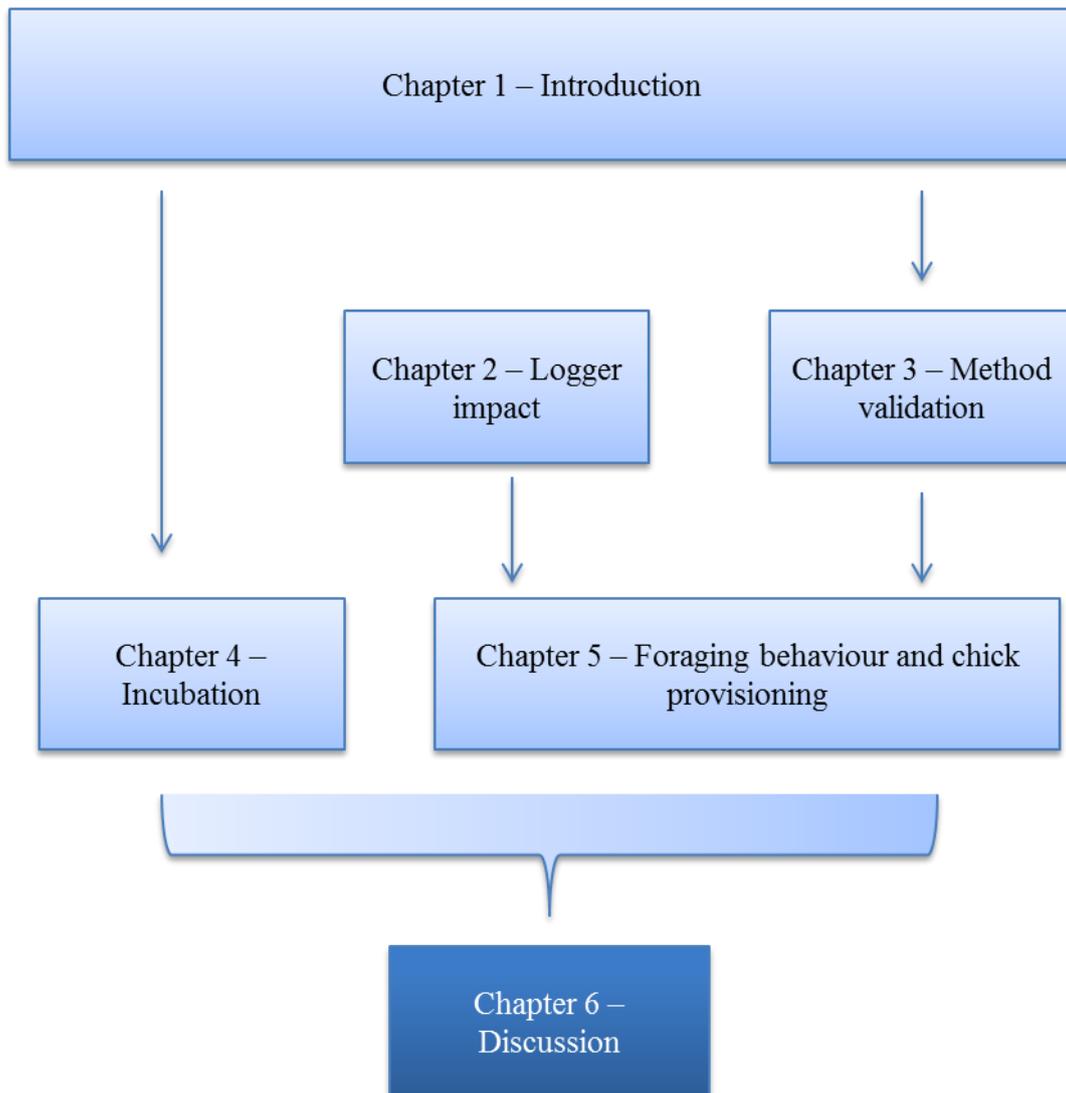
I could not directly relate stomach sample results to foraging trip duration as hard parts of prey species could be in the stomach for 6 weeks (David Cameron & Jackson 1986). Considering the main species of squid are distributed along continental shelves while the main species of fish occur in pelagic water, it is likely that Gould's Petrel forage squid during short foraging trips and fish during long foraging trips.

5.5.4 CONCLUSION

Application of geolocators provided invaluable information on movements, at-sea distribution and activity patterns of breeding Gould's Petrel. The core foraging zones of Gould's Petrel during chick rearing is bounded to waters close to the breeding colony as they need to frequently deliver food to chicks. Although there was no clear separation between short trips and a long trip like some Procellariiformes do, occasionally adults conduct a longer foraging trip to remote areas after short trips to chicks. This may be due to adult birds needing to go further to get to productive sea to replenish themselves during breeding seasons. In addition, my study implicates that behaviours of birds might be changed by food availability according to environment changes in a long term. Fortunately, variation in diet of Gould's Petrel suggests that they forage opportunistically and flexibly, which is advantageous in variable marine environments. Also changes in behaviours of parental birds consequently affect the growth of chicks. Although chicks seem to fledge successfully in a poorer condition, their long term survival might not be guaranteed. Further study on chick survival in relation to chick provision condition will be needed to support future conservation management of this threatened species.

6 CHAPTER 6 – GENERAL DISCUSSION⁵

In this chapter, I summarise the key findings of this thesis. I also discuss potential threats to the Gould's Petrel and implications for conservation of this threatened species and provide recommendations for future research.



⁵ Kim, Y., Grech, A., Priddel, D., Carlile, N, Merrick, J. R. and Harcourt, R. *In prep.* Implications for the conservation of the threatened Gould's Petrel of understanding at sea movements. . Target journal *Endangered Species Research*

6.1 INTRODUCTION

This thesis presents comprehensive behavioural analyses of reproductively active, threatened Gould's Petrel. It investigates the impact of tracking devices, tests the validity of methods for detecting parent visits, answers questions on the bird's migratory movements, documents incubation shifts in relation to body mass changes, and identifies core areas used during breeding seasons as well as key prey species.

All Procellariiformes rely on the marine environment to feed or live and only return to land to breed (Warham 1990). Given the substantial changes to both the marine environment and many of their island breeding habitats due to human activities, Procellariiformes appear particularly vulnerable to threats both on land and at sea (Schreiber & Burger 2002). Understanding their distribution at sea is therefore essential to help mitigate or remove threats such as being bycaught in fisheries (Anderson et al. 2011). During breeding, they are central place foragers, so localised threats within their foraging range may have demographic consequences at a population level (Rayner et al. 2012). For Gould's Petrel (*Pterodroma leucoptera*), which mainly breeds on Cabbage Tree Island (CTI), with a satellite colony on Boondelbah Island in Australia, protection at breeding sites together with protection at sea will enhance the effectiveness of conservation actions.

In this final chapter, I summarise the key findings of this thesis and discuss the possible threats to Gould's Petrels on both land and at sea. Chapter 6 concludes with a discussion on the implications of my research for the conservation of the Gould's Petrel and other small petrel species, and outlines recommendations for future research.

6.2 KEY OUTCOMES OF THIS THESIS

In Chapter 1, I explained the significance of gathering animal movement data, which allows for the identification of important resource areas that should be a priority for conservation. Gould's Petrel as the study species of this thesis was the subject of an investigation of breeding and foraging ecology. In Chapter 2, I undertook an experimental study and showed there was no negative impact of using small tracking devices on breeding birds, either for short- or long-term deployments. In Chapter 3, I compared multiple methods for quantifying nest attendance and demonstrated that measurements can be done in a minimally invasive manner using a variety of techniques including analysing data from temperature loggers featured in geolocators. Combining different methods was shown to be relatively efficient when faced with limited resources and to have minimum impacts on individuals, critical to research on threatened species. In Chapter 4, I reported a study of behaviour during the incubation period, which is the critical time to determine breeding success. During incubation Gould's Petrels experience significant body mass fluctuations and the condition of birds at the start of the shift and their tenacity to remain until relieved by their partner are critical to completing incubation. In Chapter 5, I identified core foraging areas of Gould's Petrels by analysing tracking data and studying diet for two breeding and incubation seasons (2011 and 2012). Gould's Petrels foraging close to breeding locations principally target cephalopods for food. As they are constrained by time to meet the energy requirements of the chicks, they do many short trips, however, to meet their own energy requirements they occasionally take longer trips further away from the breeding location. Geolocators allowed the determination of foraging areas well beyond what was previously expected and this raises important conservation concerns with regards to the potential impacts of fisheries in these areas.

6.2.1 TRACKING BIRDS

Tracking data substantially improves understanding of the pelagic distribution of seabird populations (Priddel et al., in review). Due to recent technical innovations, it is possible to attach instruments to many species of small seabirds, however, studies of the effects of tracking devices have been principally on large seabirds (e.g. Phillips et al. 2003, Passos et al. 2010), rather than on small seabirds (Rayner 2007). Given the widespread use of tracking devices for distribution and foraging research, information on how these devices may impede breeding performance is critical. In this thesis, I examined the effects of both short- and long-term deployment of geolocators on Gould's Petrel (*Pterodroma leucoptera*) at CTI, Australia during the 2010–11 breeding season. I monitored breeding adults and their chicks over short-term deployments (3 months). I found no significant effect on hatching and fledging success when a parent bird was equipped with a geocator (Chapter 2). Body mass of adults carrying geolocators declined during the breeding season, but this decline was comparable to that observed in birds without geolocators. No detectable negative impact was found for long-term (8–9 months) deployment during the non-breeding season on either the adult body mass of returning birds or their subsequent breeding performance. This finding demonstrates that tracking studies with geolocators can be conducted with confidence during both the breeding season (short-term) and in the non-breeding period (long-term). Similar verification for other small migratory seabirds fitted with geolocators is recommended for future studies.

6.2.2 MONITORING NEST ATTENDANCE

Determining nest attendance patterns of seabirds can give important insights into foraging ecology and energetic trade-offs. Previous studies have sometimes combined a number of techniques to monitor nest attendance, but there is a need to determine and compare the

reliability of measurements made by each technique. Chapter 3 focused on investigating the reliability and practicality of four different techniques (trapping adults, measuring mass change in chicks, examining images from infrared cameras and analysing temperature data from geolocators) to calculate nest attendance rates of Gould's Petrel during the breeding season. Although data sets varied in timing and duration, the calculated frequencies of nest attendance were similar. I found that each method had at least moderate agreement with other methods. However, each technique has practical limitations. The least disturbance to adult birds was from the use of infrared cameras. Temperature loggers in geolocators can be used to determine nest visits, enabling resolution of short-term foraging and provisioning behaviour. The approach of integrating data sets is recommended for studies of other small seabirds as their mass limits the devices (and thus number of sensors) they can carry.

6.2.3 INCUBATION AND CONDITION

Incubation shifts of Procellariiformes can be extremely long with breeding birds enduring long periods of fasting and significant reductions in body mass. These changes can be physically demanding and parents need to balance their energy requirements with those of their young. In Chapter 4, I assessed the incubation routine and associated changes in body mass of breeding Gould's Petrels to explore the relationships between body mass, incubation shift duration and nest desertion. The incubation routine of Gould's Petrel was similar to other Procellariiformes, albeit shift length was particularly long for a bird of this size. Egg failure was due to egg damage or nest desertion. Temporary egg abandonment was observed in both successful and failed breeders. Nest desertions generally occurred before the normal duration of the incubation shift rather than after excessively long shifts caused by the late return of the

partner. I conclude that incubation success was limited by the condition of birds at the start of the shift and their tenacity to remain until relieved by their partner.

6.2.4 FORAGING AND BREEDING PERFORMANCE

Chapter 5 described and compared the pelagic distribution of Gould's Petrel during the incubation and chick rearing period in 2011 and 2012. During incubation, tracked individuals foraged within the Tasman Sea and south of the Australian continent (Figure 5.1). After hatching, both males and females used waters close to the breeding colony (Figure 5.2). There were seasonal differences in movements of Gould's Petrel. In 2011 birds foraged in colder, more productive waters than birds in 2012 (Figure 5.3 and Figure 5.5). I found that Gould's Petrel adopt a dual foraging strategy while provisioning young. Adults alternated short trips around CTI in the western Tasman Sea with longer trips beyond Tasmania and New Zealand in the south, and to the Coral Sea and beyond in the north. Overall, 24–37% of all trips were 1–2 days in length, with a further 11–14% of trips less than 5 days in duration (Figure 5.11). Further analysis showed a relationship of slightly increased meal size with increased trip duration, but no significant difference in meal size between sexes. Stomach contents showed annual and monthly differences in their diet, which indicated a degree of flexibility in prey selection. Although there is considerable overlap in foraging zones during the chick rearing period, it is clear that an extensive range off south-eastern and southern Australia is utilised.

6.3 THREATS TO GOULD'S PETREL

Many biological and non-biological factors such as bycatch in marine fisheries and climate change threaten wide-ranging seabirds (Barbraud et al. 2012), with bycatch in fisheries being

the single greatest threat to seabirds (Anderson et al. 2011). Albatrosses, in particular, are under extreme pressure, with 17 of the 22 species threatened with extinction (BirdLife International 2012). While the direct impact of climate change on seabird populations remains unclear, global warming may have an indirect impact by reducing phytoplankton growth and overall marine productivity through reducing the upward transfer of deep, nutrient-rich water to the surface (Behrenfeld et al. 2006). Although of less overall concern, light attraction is known to cause mortality of both adults and chicks in some populations (Reed et al. 1985). On land, predation by introduced species such as rats and cats are regarded as the main threats (Le Corre 2008). In the section below, I review the key threats to Gould's Petrels and other small petrels in the context of the outputs of this thesis.

6.3.1 INTERACTION WITH FISHERIES – BYCATCH AND COMPETITION FOR PREY SPECIES

Bycatch in fisheries is of global conservation concern, with several previously abundant top marine predators experiencing sharp population declines as a result of incidental mortality (Trebilco et al. 2010, Anderson et al. 2011, Barbraud et al. 2012). Procellariiformes are highly K-selected, so mortality of a small number of breeding adults can have significant adverse impacts on the population. Nineteen of the twenty one extant albatrosses or Diomedidae, and several members of the related Procellariidae show high numbers in bycatch in many marine fisheries, resulting in high incidental mortality rate (BirdLife International, 2004a).

The global pelagic longline fishery is the world's most widespread fishing activity (Crowder & Myers 2001) and operates in Australian waters (Baker & Wise 2005). The bycatch of seabirds in longline fisheries is listed under Commonwealth (Australian) legislation as a Key Threatening Process to seabirds (AAD 2006). Seabird bycatch during longline fishing occurs

mainly during gear setting when birds ingest baited hooks or are entangled with lines at or near the surface, which results in their drowning as the gear sinks into the water (Trebilco et al. 2010). Birds are also caught during the hauling of fishing gear. Although some birds caught on the haul may be released alive, many are unlikely to survive due to severe injuries (Brothers et al. 1999). A recent study showed that 75% of seabird bycatch now occurs during hauling, as bycatch mitigation measures during setting have ensured substantial reductions in seabird mortality then (Gilman et al. 2014). The *International Threat Abatement Plan* (TAP) finalised in 1998 and revised in 2006 set an objective to reduce seabird bycatch to zero with achievable levels specified to progress this goal (AAD 2006). For Australian pelagic fisheries, such as those that operate in eastern Australian waters, these levels were set at 0.05 seabirds per 1000 hooks (AAD 2006).

The eastern tuna and billfish fishery (ETBF) expanded rapidly following the exclusion of the Japanese tuna fishery from the Australian Exclusive Economic Zone (Trebilco et al. 2010). Between September 2001 and June 2006, the majority of the reported seabird kills from the ETBF were flesh-footed shearwaters, medium to large sized albatrosses (Diomedeidae), and other shearwaters (*Puffinus* spp.). *Pterodroma* spp. dominated the remainder of the avian bycatch in the ETBF (Trebilco et al. 2010).

To improve the status of albatrosses and petrels, signatories including flag states of vessels operating in areas used by nominated species are obliged to take specific measures to protect critical habitat, control detrimental non-native species, support research and reduce incidental mortality (Phillips et al. 2006). Due to an increase in awareness of bycatch issues, the use of tracking data to identify negative interactions between birds and fisheries has been implemented (BirdLife International 2004b).

My research shows that the foraging range targeted by breeding Gould's Petrels includes large, highly productive coastal areas (Figure 5.5). Not surprisingly, these areas overlap with fisheries. For example, the area of the Southern Squid Jig Fishery (Figure 6.1) is similar to the distribution of Gould's Petrel at sea during breeding. From 2003 this fishery annually harvested more than 1200 tonne of arrow squid (*Nototodarus gouldi*) with less than 1% of catch consisting of southern calamari (*Sepioteuthis australis*), Southern Ocean arrow squid (*Todarodes filippova*) and red ocean squid (*Omnastrephes bartrami*) (DEH 2004). This could potentially lead to competition between squid fishery activity and foraging Gould's Petrel, as cephalopods are the most frequent component of stomach contents; i.e., preferred prey species. Although Gould's Petrels have rarely been sighted around boats (AAD 2006) or have not figured in bycatch associated with fishing gear (Trebilco et al. 2010), bigger Procellariiformes, such as Short-tailed shearwaters (*Puffinus tenuirostris*) and Shy Albatrosses (*Diomedea cauta*), are frequently observed around boats in Australia (Whitelaw 2002). There are three possible explanations for this: (1) Gould's Petrel may not interact with fishing boats at all as target species of the birds are different from the fishing target and their target prey size is much smaller than the fishing target size; (2) Gould's Petrel may not have been identified as it is difficult to identify small petrels unless there are experienced observers; and/or (3) due to the small breeding population (only 1000 breeding pairs), the species would be rarely observed by boats. The third possibility emphasises that even minimal incidental mortality could pose a threat to such a small population.

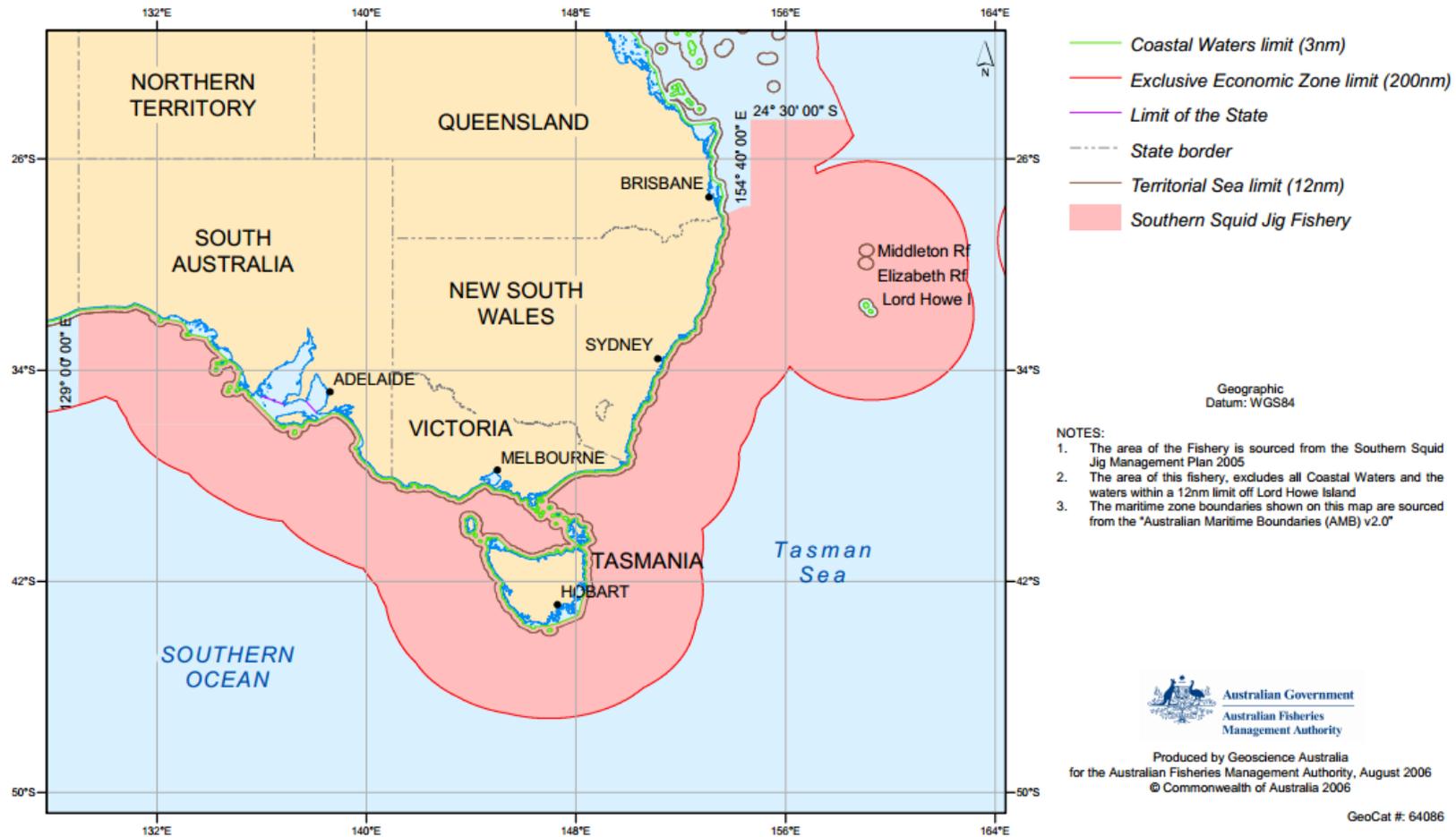


Figure 6.1 The area of the Southern Squid Jig Fishery (source: <http://www.afma.gov.au/wp-content/uploads/2010/06/ssjf.pdf>).

6.3.2 LIGHT ATTRACTION

The timing of reproduction often depends upon seasonal changes in day length (Dawson et al. 2001), and many species including birds and marine animals adjust foraging activities according to changes in the lunar cycle (Santos et al. 2010). However, these reproductive and foraging behaviours have been altered following the invention and widespread use of electrical lights (Navara & Nelson 2007). At least 21 marine species are known to be attracted to human-made lights (Reed et al. 1985). For example, the presence of artificial lights at a nesting beach of turtles can cause mortality in hatchlings by directing them away from the sea (Peters & Verhoeven 1994). Fledgling seabirds become disoriented by artificial lights while attempting to reach the sea and many eventually die due to injuries (Le Corre et al. 2002). According to a 9-year study in the Canary archipelago (Rodriguez & Rodriguez 2009), adult birds could be affected by artificial light and, in smaller species (e.g. storm-petrels), adults were more often grounded than fledglings. In addition to the negative impact of artificial light on nesting sites, lights can be threats in flyways. Each year, large numbers of migratory birds are entrapped by, and often collide with, lighthouses, large buildings and other illuminated structures (Jones & Francis 2003). At sea, light-induced bird strikes have been reported from navy vessels, cargo vessels, fishing boats and cruise ships (Bocetti 2011, Merkel & Johansen 2011).

Although concerns for light-induced mortality of the Gould's Petrel were raised in studies in New Caledonia (Le Corre et al. 2002, Croxall et al. 2012), as Cabbage Tree Island is a nature reserve, there are less concerns about the impact of light pollution compared to New Caledonia. However, Cabbage Tree Island is only 1.4 km from the entrance to Port Stephens, a popular holiday destination in the Australian summer. One accident has been reported where

a Gould's Petrel presumably attracted to bright light fell into a tennis court in Nelson Bay (Penman pers. comm.). However, so far no study has been conducted to assess the impact of light pollution on Gould's Petrel on CTI or nearby and further study on this issue is required.

A potential threat to Gould's Petrel is light pollution at sea. As Gould's Petrel mainly hunt squid that migrate to the surface during the night (Chapter 5), the bright lights on night fisheries may have a negative impact on foraging behaviour. Concerns have already been raised that the bright lights used on squid fishing boats possibly cause birds to become disorientated (AFMA 2004). To my knowledge, no study on light-induced bird strikes on vessels in Australia has been conducted, but it could be a possible threat for Gould's Petrels considering there are overlaps between their core foraging areas and frequent movements of cargo vessels and cruise ships to/from Sydney Harbour and Port Botany.

6.3.3 CLIMATE CHANGE

The potential response of seabirds to climate change remains largely unknown (Grémillet & Charmantier 2010, Barbraud et al. 2012), however, several studies have concluded that climate change poses a major threat for bird populations (Wormworth & Sekercioglu 2011). Recent studies have identified that some petrels appear to be affected by global warming (Grémillet & Boulinier 2009, Chambers et al. 2011). For example, zero or negative chick growth with low breeding success was associated with increased SST for Wedge-tailed Shearwaters breeding on islands in the Great Barrier Reef Marine Park, Australia, (Congdon et al. 2007).

Gould's Petrel is defined as a temperate species breeding on CTI, even though the island is very close to the upper boundary of the temperate zone. Whether Gould's Petrels may benefit

from an increased SST similar to other temperate species, or be negatively impacted by increased SST like subtropical species is unknown. As Congdon et al. (2007) suggest, resilience or adaptive capacity should be assessed colony-by-colony. As Gould's Petrels are a pelagic species that have more flexibility in foraging areas than inshore foragers, such flexibility is only possible if they are able to access foraging areas from nesting sites within a limited time. In 2013–14, the second highest number of breeding pairs was recorded on Cabbage Tree Island during the annual survey, however, breeding success was recorded as the second lowest breeding success due to hatching failure (Carlile pers. comm.). Albeit with very limited evidence, Gould's Petrel appears to be unable to compensate in either foraging range or target areas when conditions are poor. In 1995, poor breeding success was recorded following the loss of pilchards in South Australia (Carlile pers. comm.), where Gould's Petrel foraged during incubation period in 2011 but not in 2012 (Chapter 5). Given the variance in foraging seen in the two years of this study, it is clear that Gould's Petrel are very sensitive to environmental variability. This indicates that Gould's Petrel might suffer if climate change affects the distribution or abundance of prey species.

6.4 CONSERVATION AND MANAGEMENT OF GOULD'S PETREL

The Gould's Petrel is the rarest Australian seabird and has a restricted breeding range. A conservation program, including rabbit eradication, culling of avian predators, and the removal of Birdlime trees (that produce sticky fruits that can cause immobilisation of birds when stuck to their feathers), has led to mitigation and / or elimination of land-based threats on Cabbage Tree Island. This program recommended the establishment of new colonies to guard against deterioration in the existing breeding site due to stochastic events (Priddel & Carlile 1997a). The establishment of a satellite colony on nearby Boondelbah Island is a good

example of the use of a translocation technique to limit risk for a threatened species (Priddel & Carlile 1997a). This technique has now been successfully applied to conservation programs for other threatened seabirds such as the Bermuda Petrel (*Pterodroma cahow*) (Carlile et al. 2012) and the Magenta Petrel (*Pterodroma magentae*) (Miskelly et al. 2009).

As most of the threats on land are significantly reduced, it is likely that future threats to the conservation of the Gould's Petrel will come from issues at sea. My research has shown that the foraging areas targeted by Gould's Petrels include large, highly productive coastal areas that overlap fishery areas. The core foraging area of Gould's Petrel is not covered by marine reserves with the International Union for Conservation of Nature (IUCN) designations, nor is it covered by IA and II in the Commonwealth (Australian) network of marine protected areas (Figure 6.2), declared in 2013 (Commonwealth of Australia 2012). The categories IA and II provide the greatest restrictions to fishing and other industries (Dudley 2008, Day et al. 2012). However, these make-up less than 10% of the Gould's Petrels core areas, as identified in Figure 6.2 and in Table 6.1.

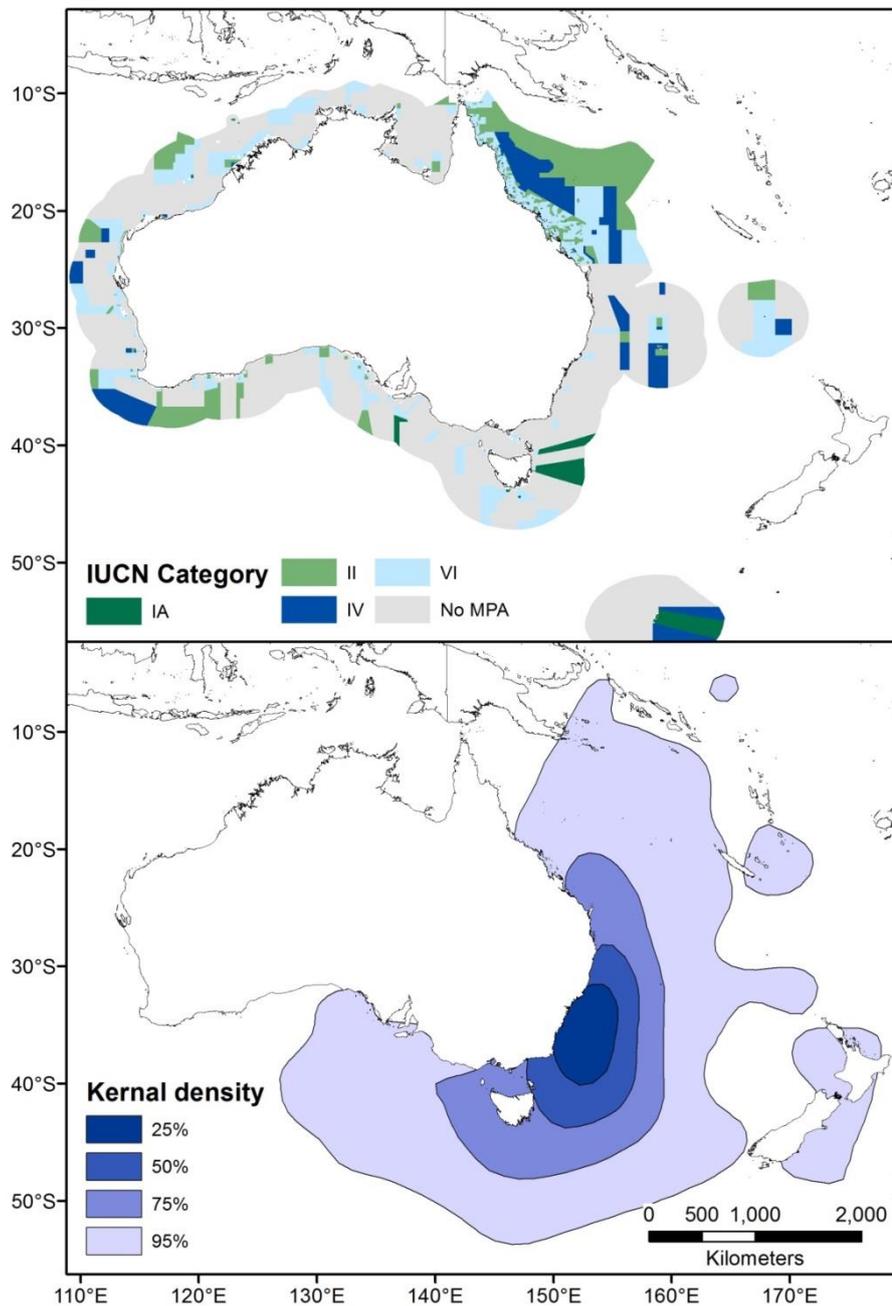


Figure 6.2 International Union for Conservation of Nature (IUCN) categories in the Commonwealth (Australian) network of marine protected areas: upper panel – IA: Strict nature reserve, II: National park, IV: Habitat/species management area, and VI: protected areas with sustainable use of natural resources; and lower panel – kernel density distribution of Gould's Petrels.

Table 6.1 Percentage of overlap of areas of kernel density contour of Gould's Petrel with International Union for Conservation of Nature (IUCN) categories IA and II in the Commonwealth (Australian) network of marine protected areas (MPA).

| Kernal density category | Total Area (km2) | Marine Reserve (IA & II) | Other Categories (IV & VI) | No MPA |
|--------------------------------|-------------------------|-------------------------------------|---------------------------------------|---------------|
| 25 | 304,016 | 3.7 | 3.8 | 92.6 |
| 50 | 359,240 | 22.0 | 12.0 | 65.9 |
| 75 | 1,084,972 | 2.8 | 34.7 | 62.5 |
| 95 | 1,845,113 | 27.1 | 32.4 | 40.6 |
| Total | 3,593,340 | 17.3 | 28.6 | 54.1 |

The lack of coverage of key Gould's Petrel at sea habitat by Australian marine reserves is of conservation concern if fishery issues arise that impact on their successful foraging. The dispersed distribution of the Gould's Petrel exposes its population to a wider range of threats, even though the deteriorating condition of one area may impact only a small proportion of the population. However, as discussed earlier, impacts on only a small number of individuals might cause population decline in such a small population as the Gould's Petrel (Chen et al. 2009). Although it will be difficult to ensure effective management of such large areas, the *Agreement of Conservation of Albatross and Petrel* (ACAP) recommends seasonal closures of important foraging areas as an effective way to reduce incidental mortality of seabirds (ACAP 2013). Although small petrels appear to have a relatively low risk of incidental mortality of seabirds bycatch (Anderson et al. 2011), extensive fisheries can reduce the prey abundance (Ramírez et al. 2013). For example, if poor breeding is expected due to sparse prey distribution during incubation, restrictions placed on squid fisheries may alleviate foraging

pressures on non-incubating partners and therefore help maintain good breeding success. However, to close the fishery temporarily, additional research on the habitat preferences of Gould's Petrels as well as other species that might use these areas will be needed. Bycatch data to show direct impact of this fishery is also needed.

There are limited studies on the impact of light attraction on Gould's Petrels. Based on studies of similar species (Rodriguez & Rodriguez 2009), it is recommended to reduce light emissions from the mainland and restrict fishing activity at night around Cabbage Tree Island during fledging peaks (from late March to mid-April) so that any negative impact on the population can be avoided. To achieve this management goal, again, further research on the impact of light on Gould's Petrel is needed.

Due to the exposure of multiple threats at sea and on land and uncertainty on the impact of climate change, actions to alleviate and/or mitigate threats to Gould's Petrel should be taken both at sea and land. For example, flesh-footed shearwaters on Lord Howe Island are afforded a high level of legislative protection on land while the population has significantly decreased due to increased bycatch in fisheries (Baker & Wise 2005, Priddel et al. 2006a).

Effective management of the large at sea area utilised by Gould's Petrel is not feasible but temporary cessation of squid fisheries in small areas could be effective. This could be difficult to implement at this stage where we do not have enough data, however, proposing Important Bird Area (*see* mIBA section below) can provide a starting point for establishing legal protections, such as Marine protected areas. Increased monitoring of the seasonal at sea hotspots would be difficult in the foreseeable future because different countries are involved in the management of areas – especially in the remote central Pacific wintering areas (Priddel et al. in review), therefore cooperation between countries is necessary. Having such a small

population spread over such a wide area has advantages as well as disadvantages. Clearly the ‘at sea’ or ‘migratory’ threats are difficult to significantly reduce in the short term, so the strategy of enhancing the output from limited breeding sites and maximising rearing success should be continued. Initiatives to minimise environmental problems at the main nesting site on Cabbage Tree Island have resulted in a significant rise in breeding numbers, but the potential for further increases in numbers at either Cabbage Tree Island or the nearby satellite colony on Boondelbah Island is very limited as the island is reaching its carrying capacity. Regional events would almost certainly have some negative effects on both these neighbouring populations so, if possible, it would be more effective to attempt to establish and nurture other more widely separated breeding populations. However, the creation of whole new populations elsewhere in Australia would involve displacement of other species breeding at these sites. At this time, management should instead focus on the small breeding groups that have been observed on Broughton Island, Little Broughton Island and Montague Islands. The logical recommendation would be to actively monitor, manage and enlarge these newly discovered nesting sites, utilising the same techniques successfully developed and implemented on Cabbage Tree and Boondelbah Islands.

6.4.1 A HOT-SPOT FOR CONSERVATION OF THE GOULD’S PETREL

Combining all location data from 2011 and 2012 presented in Chapter 5, an marine Important Bird Area (mIBA) for Gould’s Petrel was generated (Figure 6.3). The nominated area provides the following benefits for Gould’s Petrel: (a) Adults can use daily coastal north-easterly breezes to assist them to move south from the nesting location, CTI; (b) near-shore shelf upwelling, seasonal front movement with gyre circulation and some sea-mounts – especially east of Tasmania – combine to increase productivity in the south-western Tasman

Sea; and (c) frequent south-easterly winds combined with local surface wind patterns associated with large gyres (BOM 2014) assist adults returning to Cabbage Tree Island.

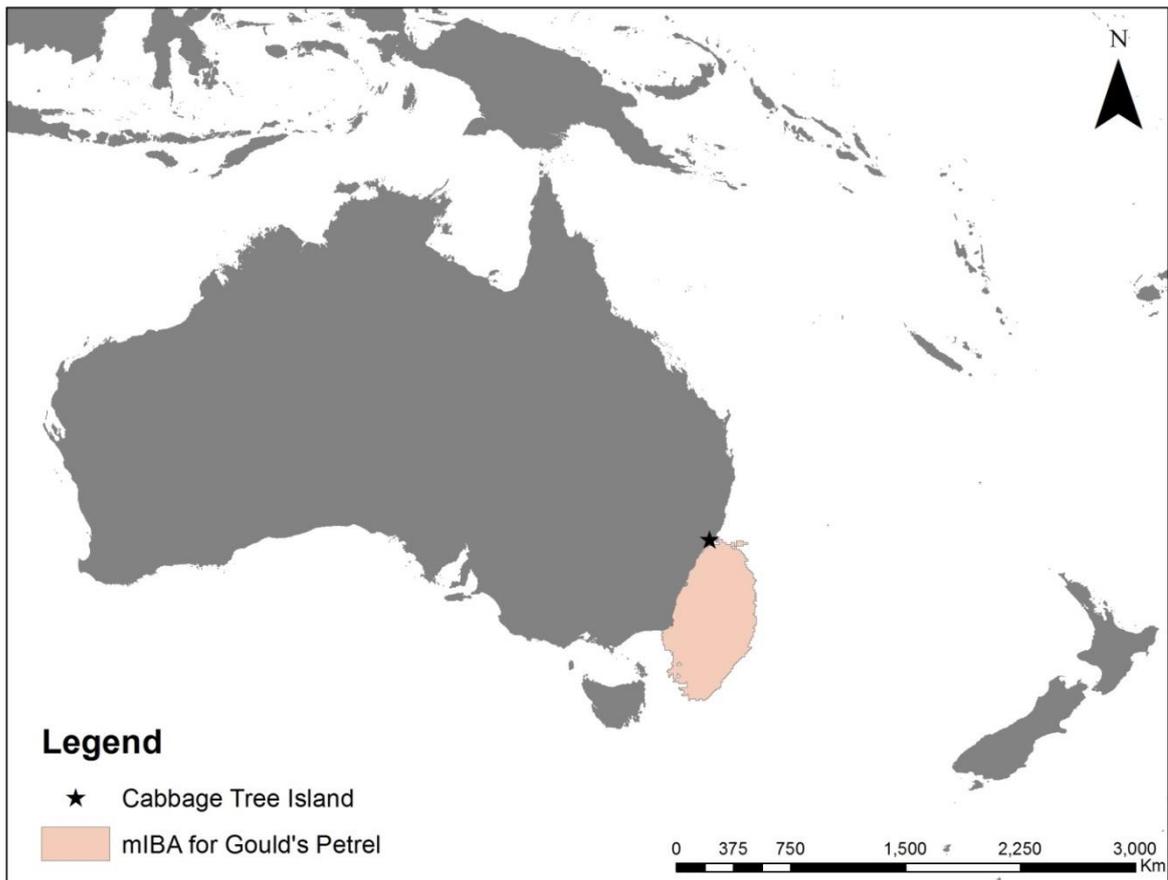


Figure 6.3 Marine Important Bird Area (mIBA) for Gould's Petrel during breeding.

There is growing evidence that the Tasman Sea and waters around New Zealand are hotspots for smaller Procellariiformes breeding in Australia and New Zealand. The nominated mIBA in the Tasman Sea (Figure 6.3) provides the protection not only for Gould's Petrel but also for other Procellariiformes that are known to utilise similar areas for foraging at some times. The Cook's Petrel (*P. cookii*), which breed mainly in New Zealand, uses the Tasman Sea and western Pacific Ocean in association with the subtropical convergence zone (Rayner et al. 2008). Black-winged Petrels (*P. nigripennis*) breed on Lord Howe Island about a month later than Gould's Petrel and occur in eastern Australian coastal waters and around north New

Zealand during the breeding season (Hutton & Priddel 2002). Therefore, temporary closures of fisheries around the identified mIBA for Gould's Petrel during the breeding season could assist not only Gould's Petrel but also other species to forage without the risk of prey loss. Although this chapter is focused on breeding season movements, the nomination of an mIBA during the non-breeding season is also necessary. Distribution of the Pycroft's Petrel (*P. pycrofti*), which breeds in New Zealand at a similar time to Gould's Petrel, is not known yet. But, during the non-breeding season, this species disperses to the central and eastern tropical Pacific (Roberson & Bailey 1991), where Gould's Petrel also spends time wintering (Appendix A). They also disperse north into the central Pacific during May–November.

6.5 FUTURE DIRECTIONS

The priority for future research on threatened species, including Gould's Petrel, should be on gathering information that directly informs their conservation. In the case of Gould's Petrel, future research should aim to obtain detailed spatio-temporal data on their movement at sea and their interactions, if any, with fisheries. It is evident through this thesis that there is annual variation in core foraging areas of Gould's Petrel. A longer duration study would provide more information on the extent of variation in the core foraging areas at different phases, and behaviours.

Chapter 4 found that egg damages are the major cause for incubation failure. This is presumably due to rocky environment on the island. Providing soft materials in artificial nest boxes might mitigate this issue. The chapter also covers the activities on the island from breeding birds during the incubation period but only part of their at sea movement during this period has been established (Chapter 5). The few poor breeding successes recorded for this species occurred during incubation, with the issues of the foraging of the non-incubating

partners likely to be the cause of failure. As incubation success is critical for breeding success, detailed studies focusing on the movements at sea during the whole incubation period is urged. Breeding success appears to decrease at old age; this, paralleled with a decrease in male survival rates, indicates that foraging ability declines with age under the effects of senescence (Weimerskirch et al. 2014). Further study on age-related foraging behavioural changes is possible with long-term banding data.

By attaching geolocators only to established breeders, as is typical of studies of small and medium-sized seabirds, my study did not include non-breeders (pre-breeders and adults that are deferring) that do not follow the same migration schedules or have the same at sea distribution (Priddel et al. in review) and may be subject to different threats. Additionally, my study could not track fledglings or juveniles at sea due to the limitations of the tracking devices and other practical reasons. The fledglings of Gould's Petrel are known to leave the colony alone, without any contact with their parents and remain at sea continuously for at least 2 years (Priddel & Carlile unpublished data). This time is critical, as it is the period when most mortality occurs (Marchetti & Price 1989, Weimerskirch et al. 2006, Riotte-Lambert & Weimerskirch 2013). Further studies tracking juveniles and non-breeders are recommended to define important bird areas at different stages of their life cycle.

As pointed out in Section 6.3.4, the information on how climate change drives potential changes in seabird population is very poor. It is important to understand how Gould's Petrels and other small petrels breeding in temperate zones are affected by climate change, how these animals respond to the changes, and if possible how to assist them to adapt to these changes.

6.6 CONCLUDING REMARKS

Wildlife research on threatened seabirds is difficult because any disturbance on the nesting site might cause further decline of the population. However, research on these species is necessary as it provides important information for their conservation. In this thesis, I provided the first insights into the distribution at sea and behaviour of the threatened Gould's Petrel, ensuring that my approach did not have any detectable negative impact on their breeding behaviour. I tested the validity of traditional and new methods to monitor the nest attendance and recommended the least invasive methods—using infrared cameras or temperature logging by geolocators.

Using the findings from my study, I identified possible threats to Gould's Petrels and other small seabirds and provided recommendations for conservation of small seabirds. These recommendations, along with the mIBA I identified through the tracking data, will be used not only for the conservation action plan for Gould's Petrel but also for an ongoing international collaborative program aimed at characterising seabird hotspots.

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8 APPENDIX A – PELAGIC DISTRIBUTION OF GOULD’S PETREL
PTERODROMA LEUCOPTERA: LINKING SHIPBOARD AND BEACHED
BIRD SIGHTINGS WITH REMOTE TRACKING DATA

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8.1 ABSTRACT

This study describes and compares the pelagic distribution and migration patterns of the two subspecies of Gould's Petrel (*Pterodroma leucoptera*), and contrasts data obtained from tracking birds at sea using geolocators with observational data (shipboard sightings, bycatch records and beach-washed specimens). While breeding, tracked individuals of both subspecies (*P. l. leucoptera* and *P. l. caledonica*) foraged within the Tasman Sea and south of the Australian continent, with forays west into the Indian Ocean prior to egg laying. After breeding, both subspecies migrated to distinct non-breeding ranges within the eastern tropical Pacific. Observational data identified the general migration pattern and foraging areas of the species, while data from geolocators provided details of migration routes and timing, core foraging ranges, and marked spatial and temporal segregation between the two subspecies. However, by attaching geolocators only to established breeders, as is typical of studies of small and medium-sized seabirds, these devices failed to identify that non-breeders (pre-breeders and adults that are deferring) may not follow the same migration schedules or have the same at-sea distribution. We conclude that integrating data from electronic tracking with observational data substantially improves our understanding of the pelagic distribution of seabird populations.

Additional keywords: at-sea sightings, foraging distribution, geographical separation of subspecies, geolocation, GLS logger, migration, New Caledonian Petrel.

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8.2 INTRODUCTION

Seabirds are more threatened, and their conservation status deteriorating faster, than any other group of birds, with approximately one third of species threatened with extinction (Croxall *et al.* 2012). Threats occur both on land at nesting sites and at sea where birds forage. The importance of secure nesting sites has long been recognised, leading increasingly to these areas being afforded legislative protection against degradation or over-exploitation. Many seabird nesting sites have been further enhanced through the eradication of alien predators, particularly rodents (Howald *et al.* 2007; Broome 2009). The situation at sea is vastly

different. Currently, less than 1% of the world's oceans have any form of legislative protection, and there is an important and immediate need to identify and delineate a network of ecologically representative Marine Protected Areas (Ronconi *et al.* 2012). Knowledge of seabird movements and behaviour is increasingly being used to identify ecologically important marine areas (e.g., Camphuysen *et al.* 2012; Le Corre *et al.* 2012; Ludynia *et al.* 2012; Montevecchi *et al.* 2012). Yet, for most seabirds, their movements at sea are poorly known. Large-scale banding programs are of limited utility in revealing patterns of seabird pelagic movements, due to the difficulty of recapture on the open ocean. Until the last two decades, shipboard surveys, bycatch records from fisheries operations, and recoveries of beach-washed specimens were the only means of identifying the pelagic distribution and movements of seabirds (Tremblay *et al.* 2009). However, such data are patchy, and collection of shipboard data is often opportunistic or prohibitively expensive, especially if vessels need to be chartered specifically for the purpose. Moreover, interpretation of sightings data can be complicated by the misidentification of morphologically similar taxa.

In the late 1990s, the advent of geolocators (Global Location Sensor or GLS logger) small enough to be carried year-round on a leg band by large birds, such as albatrosses, revolutionised the study of seabird ecology by making it possible to track individuals throughout their entire migration period (Weimerskirch and Wilson 2000; Croxall *et al.* 2005). These electronic devices record light intensity and time elapsed, and subsequent processing allows the determination of the timing of sunrise and sunset, which can then be used to calculate latitude and longitude (Phillips *et al.* 2004; Shaffer *et al.* 2005). With further miniaturisation, the development of lightweight (< 1.5 g) geolocators has made it possible to study the movements of all but the smallest seabirds without any apparent adverse effects (Catry *et al.* 2009; Quillfeldt *et al.* 2012; Rayner *et al.* 2012). Although the use of such electronic devices has increased rapidly, combining the resulting data with those obtained using traditional observational methods (i.e., shipboard surveys, at-sea collections, band recoveries from fisheries bycatch and beach-washed birds) has been identified as a high priority, since these may provide complementary information on seabird movements, with implications for conservation (Tremblay *et al.* 2009; Croxall *et al.* 2012). Such an integrated approach also provides an opportunity to compare the quality and type of information obtained from each method.

Gould's Petrel (*Pterodroma leucoptera*) is a small (~ 200–250 g) gadfly petrel that breeds on several small islands off the coast of New South Wales, Australia (Priddel & Carlile 2004b; Priddel & Carlile 2004a; Carlile *et al.* 2012), and on the main island of New Caledonia (de Naurois 1978; Bretagnolle and Shirihai 2010). The species is classified globally as *Vulnerable* (IUCN 2012). The Australian subspecies (*P. l. leucoptera*), hereafter *leucoptera*, was considered endangered under Australian legislation when the population was found to have declined to ~ 300 breeding pairs in 1992 (Priddel *et al.* 1995). However, owing to a successful recovery program, the population has since increased to ~ 1000 pairs (Priddel & Carlile 2009). Population size of the New Caledonian subspecies (*P. l. caledonica*), hereafter *caledonica*, is poorly known but population estimates of Gould's Petrel at sea in the eastern tropical Pacific (annual mean 810 000 individuals, $n = 6$; Ballance *et al.* 2002) indicate this subspecies must be substantially more numerous than *leucoptera*, though in decline due to predation by introduced Pigs (*Sus scrofa*) and Cats (*Felis catus*) (IUCN 2012). Conservation action to remove alien mammalian predators from the breeding grounds of *caledonica* has recently commenced.

The two subspecies of Gould's Petrel differ slightly in size (Bretagnolle and Shirihai 2010) and plumage (de Naurois 1978; Imber and Jenkins 1981), but are arguably indistinguishable when observed at sea. Beach-washed specimens have been assigned to subspecies based primarily on the degree of pigmentation on the inner vane of the outer rectrix: specimens with little or no pigmentation were identified as *caledonica* (Imber and Jenkins 1981). Recent phylogenetic research confirmed *caledonica* and *leucoptera* are genetically distinct at the subspecies level, although a low rate of gene flow probably occurs (Gangloff 2010).

The breeding biology of the two subspecies is similar, except the timing differs: *caledonica* breeds approximately one month later than *leucoptera*. Typically, adult *leucoptera* arrive at the breeding colony in October, lay eggs in November–December, and depart in April (Fullagar 1976). Adult *caledonica* typically arrive in November, lay eggs in December–January, and depart in May (Bretagnolle personal observation).

In the 1950s, Gibson and Sefton (1957) surmised that Gould's Petrel migrated north after breeding, though direct evidence at that time was lacking. Imber and Jenkins (1981) surveyed seabirds in the Tasman Sea annually (1970–1980) and observed Gould's Petrel only between December and April, despite similar sampling effort in other months. Additionally, beachcast specimens in New Zealand have been found only between November and June. They

concluded from this evidence that the species was probably migratory. Further, they cited eight specimens collected by Beck close to the Galapagos Islands in June 1906 as evidence of a post-breeding migration to the eastern tropical Pacific (ETP), and hypothesised a migration route that, at least in part, followed the Subtropical Front at around 40°S. Analysis of records off south-eastern Australia showed a similar seasonal trend, with the greatest numbers of observations recorded in December–April and none during June–September (Reid *et al.* 2002).

The aims of this study were to and describe and compare the pelagic distribution and migration patterns of the two subspecies of Gould’s Petrel, and to contrast the data obtained from tracking birds at sea with shipboard observations and beach-washed birds.

8.3 METHODS

8.3.1 OBSERVATIONAL RECORDS

Observations of Gould’s Petrel away from its breeding sites were obtained from published and unpublished literature, museum collection databases, other publicly-available datasets and from individual observers. The following information was extracted for each record: date, latitude, longitude, type (shipboard sighting, at-sea capture, beach-washed remains or stranded bird), number of individuals sighted and source. Where published records were presented as point locations on maps, the approximate latitude and longitude were estimated. Dubious records, duplicates and those without geographic coordinates were discarded.

Methods used to obtain at-sea sightings of Gould’s Petrel varied among sources, and included both opportunistic and systematic procedures. Fifty-eight percent of all observational records were derived from surveys conducted by the National Oceanic and Atmospheric Administration (NOAA), USA, using standard strip transect survey procedures detailed in Ballance (2006). Other systematic surveys that contributed large datasets used similar techniques.

8.3.2 GEOLOCATORS

Twenty-two BAS geolocators (MK14, British Antarctic Survey, UK) and 20 Lotek geolocators (NanoLAT2900, Lotek, Canada) were attached to adult *leucoptera* in March 2010

when they were provisioning nestlings on Cabbage Tree Island, Australia (32°41'18"S, 152°13'28"E). All Lotek, and all but one of the BAS geolocators were retrieved between November 2010 and January 2011 when adults returned to their nests to breed. However, 11 BAS geolocators and 8 Lotek geolocators failed to record more than a few weeks of data. Information collected from the 22 fully functional geolocators covered the non-breeding period from late chick-rearing to incubation the following breeding season. Movements during breeding (late incubation to fledging) were tracked by attaching Lotek geolocators (NanoLAT2900, Lotek, Canada) to 32 breeding birds between December 2011 and April 2012.

The pelagic movements of *caledonica* were tracked using BAS geolocators. These were attached to 17 adult *caledonica* incubating eggs on Grande Terre (21°20'S, 165°30'E), the main island of New Caledonia, in January 2010. Seven geolocators were retrieved in January 2011.

Both subspecies were caught by hand at the nest. Geolocators were attached with cable ties and glue to a plastic (darvic) leg band fitted around the tarsus of the bird. The total weight of geolocator, leg band and attachment material was equivalent to < 1.2% of adult body mass. Similar attachment methods have been used in other studies, with no detrimental effects reported (Rayner 2007; Carey 2011). The attachment of geolocators to Gould's Petrels had no discernible effect on hatching success, fledging success, fledging weight or parental weight (Kim *et al.* in press).

BAS geolocators measured ambient light level every 60 sec and then logged the maximum value for each 10 min interval. Light data were processed using TransEdit software (Jensen Software Systems) as described by Fox (2009) to provide two locational fixes per day. Longitude was calculated from the time of local noon and midnight relative to Greenwich Mean Time, based on sunrise and sunset times inferred from light curve thresholds. Latitude was calculated from day length. However, latitude cannot be computed during periods close to the equinoxes because day and night are of approximately equal length uniformly across the globe. Therefore, locations occurring within 3 weeks of the equinoxes (20 March and 23 September) were excluded. A previous study of a free-ranging seabird indicated a mean error of c. 200 km for data from BAS loggers (Phillips *et al.* 2004).

Lotek geolocators functioned on a similar principle to BAS geolocators but incorporated onboard processing of the light data to compute latitude and longitude (one location per day). They also recorded sea-surface temperature when birds were resting on the water, which was combined with satellite imagery (mid-wavelength infrared), where available, to estimate latitude during the 3 weeks either side of the equinox using LATVIEWER (Lotek, Canada). The mean error using this approach (c. 200 km) is broadly similar to that of BAS geolocators (Shaffer *et al.* 2005).

8.3.3 ANALYSIS OF LOCATION DATA

We removed from the data set any locations that involved movements of > 1600 km in a single day, those with interruptions to light curves around sunset and sunrise, and any that were clearly outside the known or possible range of Gould's Petrel. Locations were then pooled across individuals to estimate year-round utilisation distribution (UD) kernels for each subspecies following methods detailed in Shaffer *et al.* (2009). A 1000-km buffer around each colony was used to define the extent of the breeding range (Rayner *et al.* 2008), and the 80% contour of UD kernels, calculated individually, were used to define the non-breeding range for each bird (Guilford *et al.* 2009). Dates of the first and last locations to enter and exit the breeding and non-breeding ranges were used to determine the timing of migration for each individual. Dates when individuals first entered their burrows were identified by periods of darkness recorded during the day (see Rayner *et al.* 2011). Dates and duration of migration were compared between subspecies using *t*-tests that do not assume equal variances (Welch 1947). All means are presented \pm standard deviation.

8.4 RESULTS

8.4.1 OBSERVATIONAL DATA

A total of 2036 observational records (2588 individual birds) were collated (Table 1). These comprised 1881 shipboard sightings, 31 records of birds collected (killed) at sea, and 124 records of beach-washed birds including seven live emaciated individuals. Records spanned the period 1906–2012 and were obtained from the following sources: databases (81.3%), publications (10.1%), museum records (5.1%) and individual observers (3.5%).

INSERT TABLE 1 HEREBOUTS

At-sea observations (shipboard sightings and collections) were concentrated in the Tasman Sea and in the ETP between Hawaii and the Galapagos Islands (Figure 1). The remaining records were off the eastern and southern coasts of Australia and off New Zealand, and in the Coral Sea, the Indian Ocean to the south of Australia, and the Southern Ocean as far south as the coast of Antarctica. There was a strong seasonal trend (Figure 1). During December–April (breeding season), records were largely confined to the Tasman Sea and Indian Ocean south of Australia (Figure 1A). During May–August (non-breeding season), most sightings were in tropical latitudes of the central and eastern Pacific Ocean, with a small number in the Tasman Sea (Figure 1B). During September–November (pre-laying phase of the breeding season), sightings extended across the tropical Pacific Ocean, Tasman Sea and Indian Ocean, with some in the Southern Ocean close to Antarctica (Figure 1C). Sightings south of latitude 55°S ($n = 19$) were recorded only during September–March, but typically few ships (observers) are present in these cold waters outside these warmer months. Within the ETP, sightings were concentrated between 10°N and 10°S latitude, and from 90°W to 150°W longitude. Survey effort within the ETP extended further to the north, east and west of these sightings, but not to the south (Figure 2).

INSERT FIGURE 1 HEREBOUTS

INSERT FIGURE 2 HEREBOUTS

Records of beach-washed birds were from Australia ($n = 68$) and New Zealand ($n = 36$). Australian recoveries were from Tasmania and the coasts of southern and south-eastern mainland Australia in all months except July (61% of 56 live or recently dead birds were recorded in January–March). All but one of the New Zealand birds were collected from the west coast of the North Island in November–June. Overall, 41 beach-washed birds had been identified to subspecies: 79% from Australia ($n = 24$) were *leucoptera*, whereas 94% from New Zealand ($n = 17$) were *caledonica*. Of specimens collected at sea, 10 from the Tasman Sea and one from near Tonga were identified as *caledonica*. Further, Spear *et al.* (1995) described eight birds (of 70) collected in the ETP as ‘*leucoptera*-type’ based on the same criterion.

Within the Tasman Sea and Indian Ocean, Gould’s Petrels were uncommon and usually encountered singly (mean group size = 1.7 ± 1.2 , $n = 258$; Australian Antarctic Database), and

only rarely in groups of six or more birds. Within the ETP, Gould's Petrel was one of the most common petrels observed, but again was frequently encountered singly (mean group size = 1.2 ± 1.1 , $n = 1284$; NOAA Database).

8.4.2 TRACKING DATA: P. L. LEUCOPTERA

The 22 functional geolocators retrieved from *leucoptera* recorded data for a mean period of 252 ± 11 days (239–275 days) and provided a total of 4277 filtered locations. All *leucoptera* that carried geolocators during the breeding season successfully reared chicks to fledging.

Locations of the 22 individuals tracked after breeding were concentrated in equatorial waters of the central Pacific Ocean (Figure 3A), predominantly south of Hawaii (20°N – 20°S , 140 – 170°W) and between Hawaii and Japan (20°N – 40°N , 160 – 170°E). Individual birds began the post-breeding migration on 04 April ± 6 days and travelled eastward then north/northwest to reach their non-breeding range on 24 April ± 10 days (Table 2), after 22.6 ± 8.1 days (Table 3). The average maximum distance from the breeding site was $9,355 \pm 1584$ km. Birds remained in their non-breeding ranges for 141.3 ± 17.6 days (Table 3), departing on 14 September ± 19 days (Table 2) to undertake a return migration westward to eastern Melanesia then southward into the Tasman Sea. Birds completed this return migration in 27.0 ± 16.3 days (Table 3), arriving at waters around the colony on 12 October ± 6 days (Table 2).

INSERT FIGURE 3 HEREBOUTS

INSERT TABLE 2 HEREBOUTS

Birds first visited their burrow on 18 October ± 6 days (Table 2). In November, shortly before laying, birds foraged in the Tasman Sea and waters to the south of Australia, with one individual going west into the Indian Ocean, as far as 100°E . During the incubation and provisioning period, the core foraging area (Figure 3A) was in the Tasman Sea along the east coast of mainland Australia and around Tasmania.

8.4.3 TRACKING DATA: P. L. CALEDONICA

The seven functional geolocators retrieved from *caledonica* recorded data for a period of 347 ± 3 days (342–349 days) and provided a total of 1872 filtered locations. Locations of the seven individuals tracked after breeding were concentrated in equatorial waters of the eastern

Pacific Ocean (Figure 3B), predominantly west and southwest of the Galapagos Islands (0°S–20°S, 90–140°W). Birds departed their breeding range on 25 March \pm 30 days and travelled eastward, passing the north of New Zealand before bearing north to reach their non-breeding range on 18 May \pm 13 days (Table 2) after 54.6 ± 24.5 days (Table 3). The average maximum distance from the breeding site was $10,083 \pm 1279$ km. The birds remained in their non-breeding ranges for 135.9 ± 31.1 days (Table 3), departing on 4 October \pm 24 days (Table 2) to undertake a return migration westward to Melanesia then southward into the Tasman Sea. Birds completed this migration in 30.7 ± 19.3 days (Table 3), arriving at their breeding range on 4 November \pm 7 days (Table 2).

INSERT TABLE 3 HEREBOUTS

Birds first visited their burrow on 6 November \pm 8 days (Table 1). In November, shortly before laying eggs, six of the seven birds foraged in the Indian Ocean to the south and southwest of Australia, as far west as 100°E. The remaining bird travelled no further west than Tasmania (145°E). All birds then contracted their range to a core foraging area in the central Tasman Sea for the duration of the breeding period (Figure 3B).

8.4.4 BREEDING PHENOLOGY

The mean date of departure from the breeding range was 10 days earlier for *caledonica*; however, the range in dates of *caledonica* encompassed those of *leucoptera* and this difference was not significant ($P = 0.413$). The variance in the date of departure from the breeding range was particularly high for *caledonica* (65 days compared to 25 days for *leucoptera*); differences between subspecies in the variance of other departure and arrival dates were 5 days or less (Table 1). The high variability in departure date for *caledonica* is because two tagged individuals left the colony early (February cf. April), presumably after failing in their breeding attempt. These failed breeders spent the next two months in the Tasman Sea and in waters to the south of Australia before arriving at the non-breeding ranges at about the same time as successful breeders. Consequently, the duration between leaving the breeding range and arriving at the non-breeding range (termed here as the duration of post-breeding migration) was longer and more variable for *caledonica* than for *leucoptera* (Table 2).

On average, *leucoptera* arrived at their non-breeding ranges 24 days earlier than *caledonica* (Table 1). Both subspecies spent a similar amount of time in the non-breeding range (approximately 140 days, Table 2), with *leucoptera* departing 19 days earlier than *caledonica* (although this difference was not significant: $P = 0.091$, Table 1). The duration of the return migration was similar for each subspecies (Table 2), with *leucoptera* arriving at the breeding range 23 days earlier than *caledonica*, and first visiting the nest burrow 19 days earlier (Table 1).

8.5 DISCUSSION

This study provides the first clear insight into the pelagic distribution and migration pattern of Gould's Petrel, during both the breeding and non-breeding periods. The integration of sightings at sea with data from remote tracking has demonstrated that this threatened seabird has a seasonal reliance on two discrete oceanic regions: the Tasman Sea and waters to the south of Australia during breeding, and the tropical Pacific during non-breeding.

8.5.1 SPATIAL AND TEMPORAL SEPARATION OF SUBSPECIES

Both subspecies of Gould's Petrel are trans-Pacific migrants. Although the at-sea distributions of the two subspecies overlap, there is a high degree of spatial and temporal separation. This segregation is probably one of a number of mechanisms that may reduce the level of intra-specific competition for resources (Pitman and Jehl 1998; Croxall *et al.* 2005; Phillips *et al.* 2005).

As in other small *Pterodroma* species (e.g., Rayner *et al.* 2012), both subspecies of Gould's Petrel returned to waters around the breeding colony approximately one month before laying, and within a few days visited the burrow. During the breeding season (including the pre-laying, incubation and chick-rearing periods) the core foraging areas of *leucoptera* were close to Australia, whereas those of *caledonica* were midway between Australia and New Zealand. The more-easterly distribution of *caledonica* is consistent with observations; almost all (94%, $n = 17$) beach-washed specimens in New Zealand, as well as the only bird collected in the eastern Tasman Sea, have been identified as this subspecies. Given that both taxa probably occupy the same pelagic foraging niche, this difference in distribution may be linked to the central-place constraints associated with breeding (Orians and Pearson 1979). Like all breeding seabirds, Gould's Petrels must return to their nest at regular intervals for incubation

and chick provisioning, and are thus restricted to foraging within a certain distance from the breeding colony.

After breeding, both subspecies migrated to the tropical Pacific. The distribution of at-sea observations of Gould's Petrel within the ETP appears to be generally coincident with the eastward-flowing North Equatorial Countercurrent, though clearly many individuals were also associated with the westward-flowing South Equatorial Current (Fiedler and Talley 2006). There appears to be an absence of birds in the general region of the Equatorial Front, supporting distribution patterns for piscivorous seabirds that have been proposed for this area in general (Ballance *et al.* 2006). Data obtained by geolocators provided insight into the at-sea sightings by revealing subspecies-specific associations with different currents. The foraging range of *caledonica* was concentrated in equatorial waters of the eastern Pacific (90–140°W), predominately at latitudes south of the equator, in waters influenced by the westward flowing South Equatorial Current. Ribic and Ainley (1997) also documented an association between Gould's Petrel and the South Equatorial Current, particularly during El Niño–Southern Oscillation events. In contrast, the foraging range of *leucoptera* was concentrated in the central Pacific (140–170°W), several thousand kilometres west of that of *caledonica*, and north of the equator in waters primarily influenced by the North Equatorial Current. Thus, the association of this species with both currents evident in the sightings data may be explained by subspecies-specific associations that represent distinct preferences for different currents, apparent in the geolocator data.

Migration schedules of the two subspecies were asynchronous: *leucoptera* arrived at the breeding and non-breeding areas approximately three weeks before *caledonica*. Consistent with their migration timetables, breeding of the two subspecies was also asynchronous (Figure 4): *caledonica* first visited the burrow about three weeks later than *leucoptera*. The high variation among *caledonica* in the time of their departure from the breeding grounds was indicative of a high incidence of nesting failure, with many adults leaving long before chicks normally fledge. Deploying geolocators on *caledonica* earlier in the breeding cycle (when incubating eggs or brooding young chicks) compared to *leucoptera* (when feeding well-grown chicks) may have contributed to us recording a greater failure rate for *caledonica*, although higher rates of predation in New Caledonia (see below) may also have played a role.

INSERT FIGURE 4 HEREABOUTS

When migrating across the South Pacific, both subspecies travelled about 20,000 km or more in a counter-clockwise direction, moving eastward at high southern latitudes (approximately 45–55°S) and returning at lower equatorial latitudes. These tracks overlap with part of the migration routes of several other seabirds that migrate across the South Pacific, including the sooty shearwater *Puffinus griseus* (Shaffer *et al.* 2006), Cook’s Petrel *Pterodroma cookii* (Rayner *et al.* 2011) and Westland Petrel *Procellaria westlandica* (Landers *et al.* 2011). These species presumably take advantage of the prevailing winds to conserve energy, similar to trans-equatorial migrants in the Atlantic Ocean (Felicísimo *et al.* 2008; Egevang *et al.* 2010).

8.5.2 COMBINING TRACKING AND OBSERVATIONAL DATA

Until this study, our understanding of the pelagic distribution of Gould’s Petrel was based on the interpretation of observations at sea and beach-washed specimens. Although such records are patchily distributed, both temporally and spatially, collectively they do elucidate the main features of the at-sea distribution of Gould’s Petrel (albeit both subspecies combined) revealed by tracking. There are, however, some substantial differences in the findings obtained using the two techniques.

Shipboard observations during breeding (*leucoptera*: October–March; *caledonica*: November–April) showed a concentration of foraging in the Tasman Sea, with some sightings in the waters south of the Australian continent as far south as the Antarctic shelf (mainly November–December) and beyond the western extremity of the continent. Tracking over the same period revealed a similar pattern of movements, except that birds with geolocators did not travel to Antarctic waters. Tracking did, however, identify that foraging to the west of Australia involved breeding adults prior to egg laying and, *contra* Surman *et al.* (1997), these birds are more likely to be *caledonica* than *leucoptera*. The lack of tracking records in Antarctic waters is at odds with shipboard observations. Possible misidentification of sightings in the Southern Ocean is unlikely as Gould’s Petrel is readily distinguishable from other small- or medium-sized gadfly petrels found there by the diagnostic blackish-brown hood (head to upper mantle and breast sides) contrasting with the grey lower mantle/back and white underside (Shirihai 2007). Furthermore, there are numerous records spanning many years ($n = 18$, 1982–2001), so misidentification would have had to involve numerous observers, which seems unlikely. We suspect that birds at polar latitudes during the breeding season are non-breeders (pre-breeders and adults that failed early or are deferring) foraging in

highly productive waters, unencumbered by the need to return regularly to a breeding site. The deployment of geolocators only on breeding birds would then explain why no tracked bird was recorded foraging this far south. Alternatively, the difference could be a response to interannual variation in prey distribution and abundance.

Sightings of birds in the eastern tropical Pacific between late July and late November, along with identification of some individuals to subspecies level, correctly suggest that *caledonica* migrate across the Pacific after breeding. However, whether *leucoptera* also migrate to the eastern tropical Pacific is not clear from the at-sea observations, as no specimens confirmed as this subspecies have been recorded far from the breeding grounds in eastern Australia. Two imprecise records involving nine individuals (see *Results*) are the only observational evidence to suggest that *leucoptera* ventures into the tropical Pacific. Thus, observational data failed to differentiate the migration path and foraging grounds of *leucoptera*. The two subspecies are difficult to distinguish at sea and their distributions overlap, hindering our understanding of their pelagic distributions based on sightings alone.

The distribution of Gould's Petrel in the eastern tropical Pacific based on sightings data does not correspond well with the tracking data. This is because the geographical extent of the shipboard surveys did not extend any further south or west than the cluster of sightings shown in Figure 2 and most sightings were at the southern limits of the survey area. Despite such limitations, at-sea sightings can provide information about foraging behaviour that is not attainable with geolocators. For example, observations of group size at sea indicate that Gould's Petrels are solitary foragers, while both breeding and non-breeding. There is no evidence that this species congregates in groups to forage on locally abundant prey, suggesting that their prey is diffuse across broad expanses of ocean. Other *Pterodroma* species (e.g., Barau's Petrel *Pterodroma barau*) and indeed other tropical seabirds (e.g., Wedge-tailed Shearwater *Puffinus pacificus*) similarly seem to have large non-breeding ranges and presumably also target diffusely distributed prey during the non-breeding season (Catry *et al.* 2009; Pinet *et al.* 2011).

All tracked individuals migrated and, apart from the early departure of presumed failed breeders, the timing was largely synchronous within each subspecies. However, sightings of individuals in the Tasman Sea in all months except June suggest migration timing may be staggered in birds of differing status. Birds that migrate late or not at all, we suggest, are likely to be non-breeders (immature birds or mature birds taking a sabbatical from breeding)

that are not tied to the colony, and so do not need to follow rigid migration schedules and patterns. Non-breeders can account for a substantial proportion of the Gould's Petrel population (Priddel *et al.* 1995), thereby explaining much of the variation associated with observational data. Failed breeders, as evidenced by the tracks of a few *caledonica*, do undergo post-breeding migration, but their movements are less direct than their successful counterparts. Consequently, although they leave the breeding range earlier than successful breeders, they arrive at the non-breeding range at about the same time.

Unlike satellite-linked devices, geolocators need to be retrieved before data can be accessed, so they are typically attached only to breeding birds that are likely to be recaptured because of their high nest-site fidelity. By targeting only established breeders, the use of geolocators failed to identify that some Gould's Petrels forage in Antarctic waters or do not follow the standard migration timetable. Such discrepancies are presumably attributable to non-breeders (pre-breeders or deferring breeders). The survival rate of immature individuals is a key component of the demography of long-lived species like seabirds, and an important aspect of their life history that should not be overlooked. Consequently, studies of the pelagic distribution of seabirds should, where possible, involve all stages of the life cycle.

Through combining tracking data acquired over a single year with historical observations collected over a century, this study revealed the at-sea distribution and migration patterns of Gould's Petrel in unprecedented detail. Sightings identified only the general migration pattern and foraging areas of the species, while data from geolocators provided substantially more information by clarifying migration routes and timing, delineating core foraging areas, and revealing marked spatial and temporal segregation between the two subspecies. Geolocator deployments, however, might not reveal the full spatial or temporal variance associated with the distribution of a species at sea unless immatures and deferring breeders (and perhaps failed breeders) are also sampled. However, deploying geolocators on birds in these status groups is problematic due to the difficulties associated with retrieving devices from individuals that are not obliged to return to a particular nesting site and, particularly in the case of fledglings, also tend to show lower survival. Data on the pelagic distribution of immature and deferring birds were generally only available through shipboard observations, and although a number of recent tracking studies have targeted these life history stages, they are mainly limited to large, surface-nesting species (Phillips *et al.* 2005; Alderman *et al.* 2010; Votier *et al.* 2011; Péron and Grémillet 2013; Riotte-Lambert and Weimerskirch 2013;

Gutowsky *et al.* 2014). We conclude, therefore, that integrating data from electronic tracking with shipboard observations substantially improves our knowledge of the pelagic distribution of seabird populations at all life history stages, particularly in those species that lack distinct juvenile plumage.

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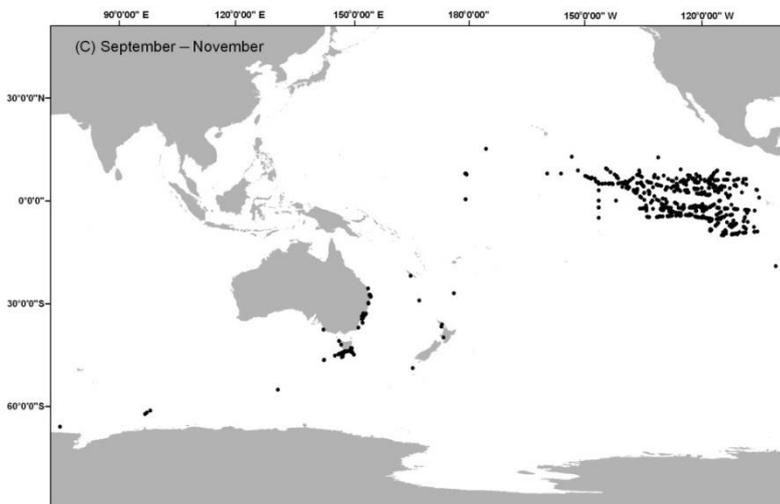
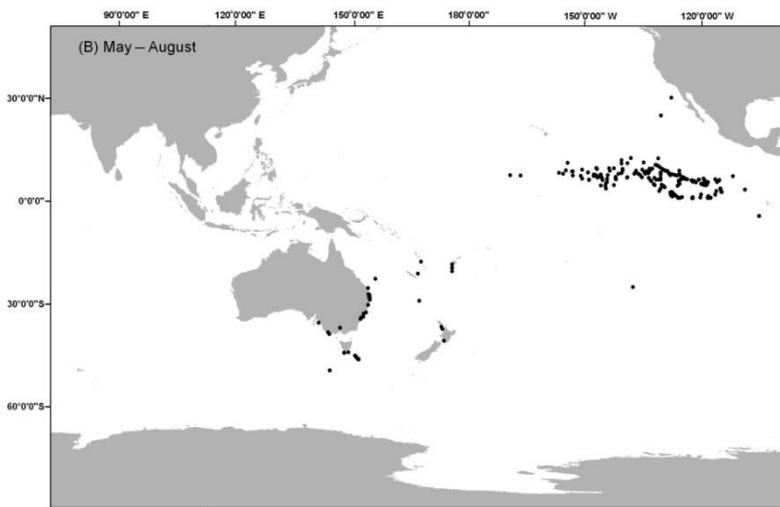
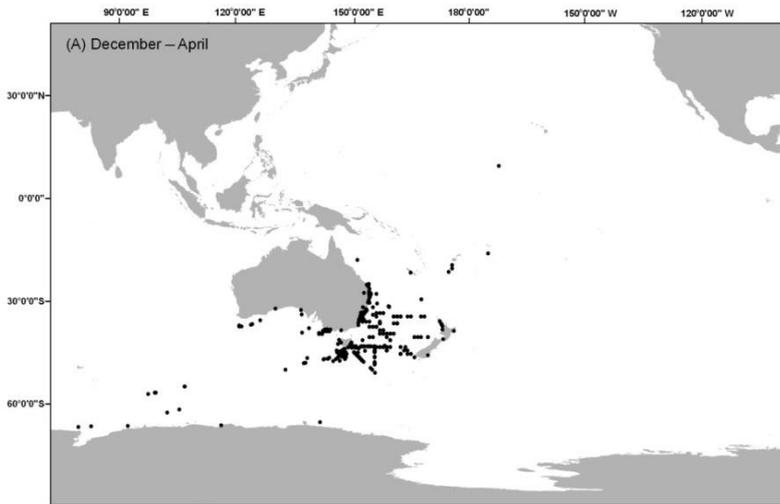
8.8 FIGURE LEGENDS

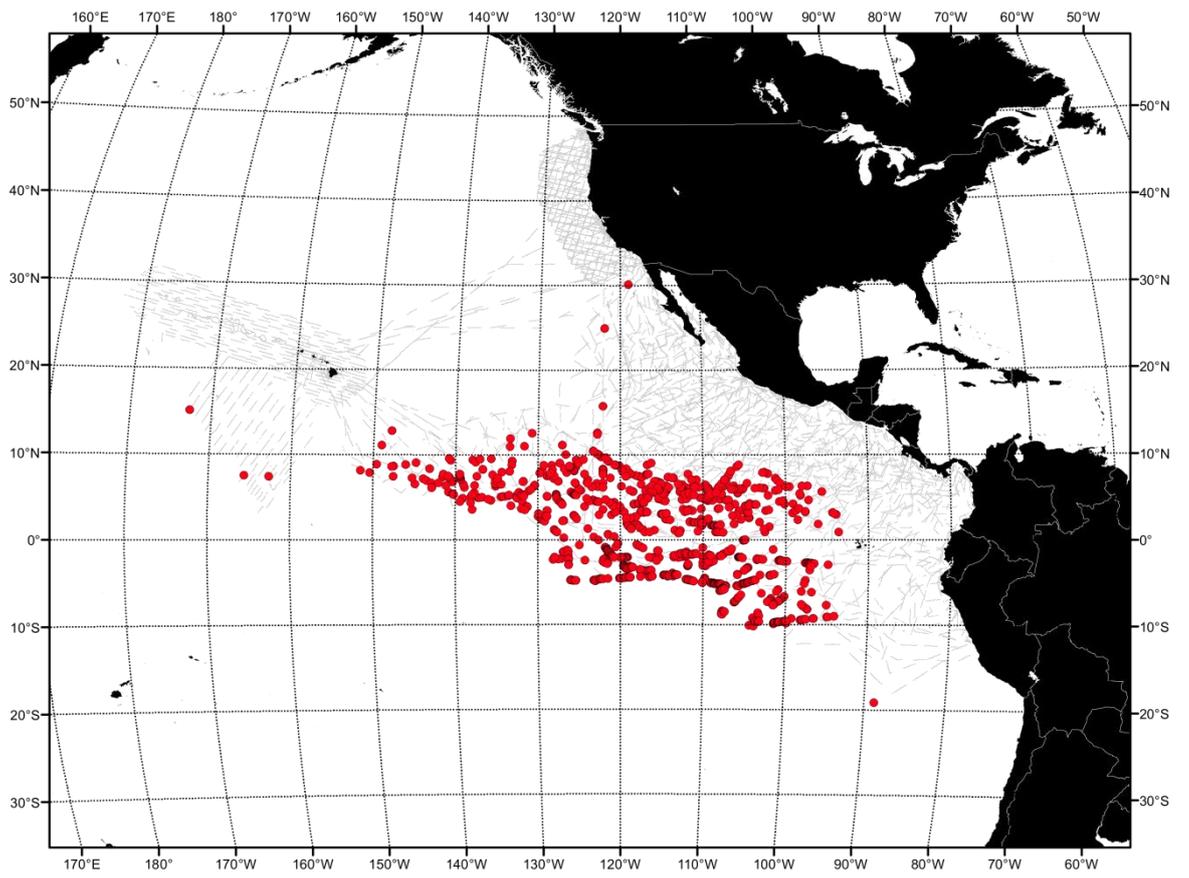
Figure 1. Locations of shipboard sightings of Gould's Petrel ($n = 1881$), beach-washed birds ($n = 124$), and individuals collected at sea ($n = 31$) during (A) December–April, (B) May–August and (C) September– November.

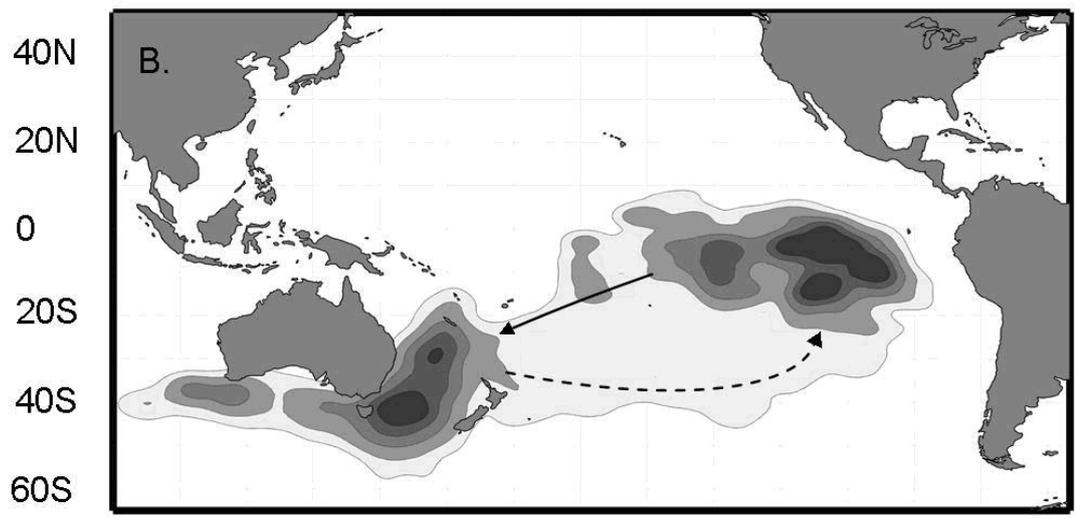
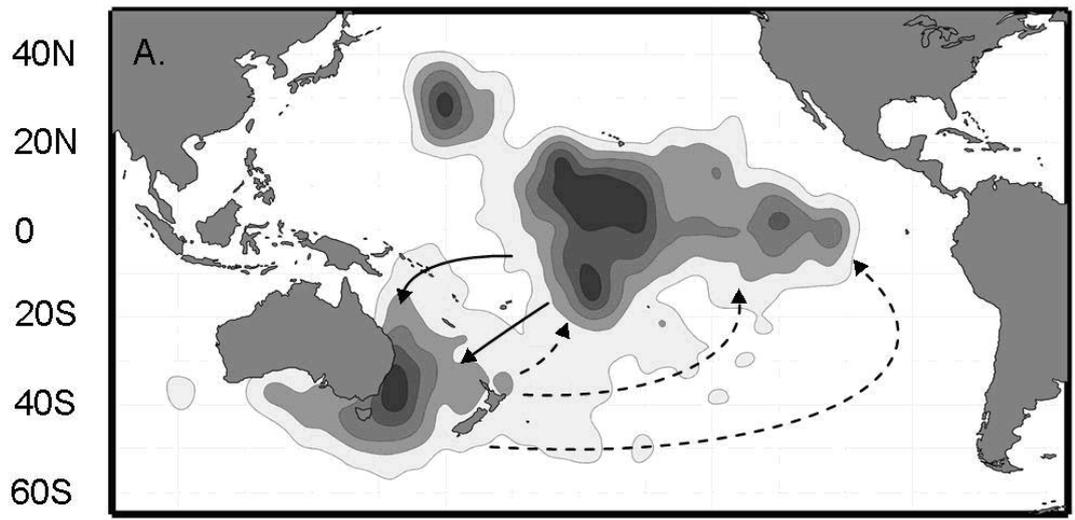
Figure 2. Locations of shipboard sightings of Gould's Petrel in the eastern Pacific during surveys undertaken by NOAA ($n = 1180$). Grey lines indicate the track lines of survey vessels. Surveys were undertaken August–November in the eastern tropical Pacific (1988–1990, 1998–2000, 2003, 2006), central Pacific (2002, 2005, 2010), and California Current (2001, 2005, 2008). A single observer seated in the flying bridge and using handheld binoculars counted all seabirds within a 300-m strip transect on one side of the ship travelling at 18.5 km hr^{-1} (10 knots).

Figure 3. Kernel density distributions for (A) *P. l. leucoptera* and (B) *P. l. caledonica* tracked with geolocators from March 2010 – February 2011 and January 2010 – January 2011, respectively. Shaded polygons represent the 20, 40, 60, 80 and 95% density contours. The approximate post-breeding (dashed lines) and pre-breeding migration (solid lines) paths are shown. Breeding and non-breeding ranges were defined as those areas enclosed by the 80% contour lines.

Figure 4. Migration schedule of the two subspecies of Gould's Petrel, as revealed by geolocators. Post-breeding migration begins on departure from the breeding range and concludes on arrival at the non-breeding range. Pre-breeding migration is the return journey. The date of the first visit to the nesting burrow is also shown. Vertical lines indicate means; shaded areas show the range.







120E 150E 180 150W 120W 90W

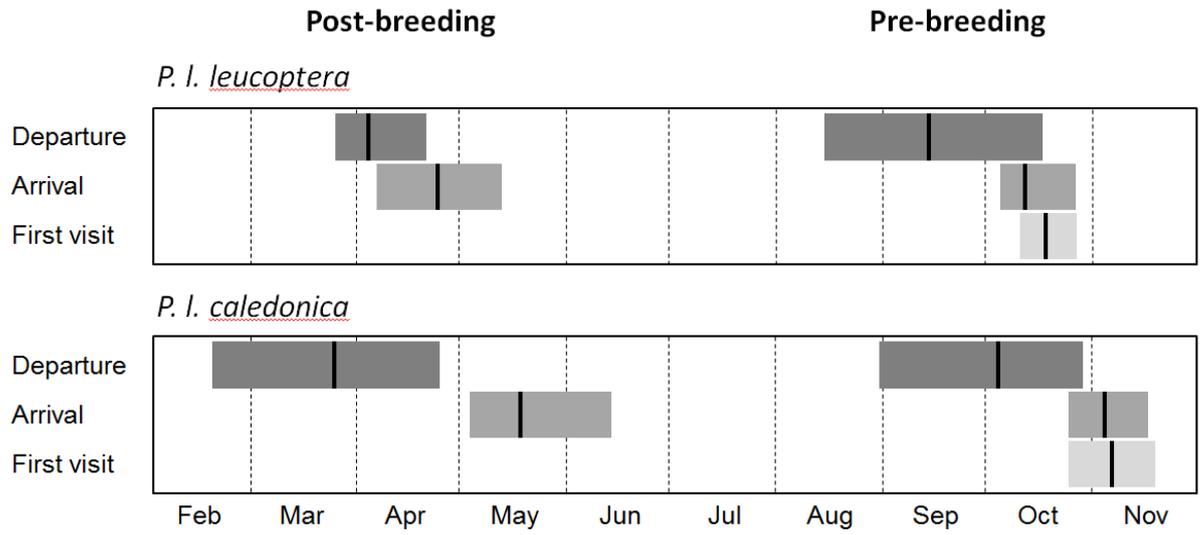


Table 1. Sources of observational data: beach-washed birds, birds collected at sea, and shipboard sightings

Figures indicate number of records (excluding duplicates).

| Source | Beach-washed | Collected at sea | Sighting | Total |
|---|--------------|------------------|----------|-------|
| Museums | | | | |
| American Museum of Natural History | 1 | | | 1 |
| Auckland Museum | 9 | | | 9 |
| Australian Museum | 12 | | | 12 |
| Australian National Wildlife Collection | 3 | | | 3 |
| Bernice Pauahi Bishop Museum | | 2 | | 2 |
| California Academy of Sciences | | 3 | | 3 |
| Museum Victoria | 6 | | | 6 |
| National Museum of Natural History | | 21 | | 21 |
| Queensland Museum | 30 | | | 30 |
| Queen Victoria Museum | 2 | | | 2 |
| South Australian Museum | 5 | | | 5 |
| Tasmanian Museum and Art Gallery | 1 | | | 1 |
| Museum of New Zealand Te Papa Tongarewa | 5 | 1 | | 6 |
| Western Australian Museum | 2 | | | 2 |
| Databases | | | | |
| Australian Antarctic Data Centre | | | 307 | 307 |
| BirdLife Australia Birdata | 20 | | 25 | 45 |
| British Antarctic Survey | | | 1 | 1 |
| Avian Knowledge Network, Cornell Lab of Ornithology | | | 35 | 35 |
| Eremaea Birds | | | 46 | 46 |
| National Oceanic and Atmospheric Administration | | | 1180 | 1180 |
| Atlas of NSW Wildlife | | | 34 | 34 |
| South Australia Fauna Observations | | | 8 | 8 |
| Publications | | | | |

| | | | | |
|------------------------------|-----|----|------|------|
| Barton (1980) | | | 4 | 4 |
| Blaber (1986) | | | 7 | 7 |
| Bull (1943), (1946) | 2 | | | 2 |
| Edgar (1972) | 1 | | | 1 |
| Gibson (1977) | 3 | | | 3 |
| Gibson and Sefton (1957) | 1 | | | 1 |
| Gosper (1981) | 2 | | | 2 |
| Green (1984) | 1 | | | 1 |
| Hawke (1989) | 1 | | | 1 |
| Hindwood and Serventy (1943) | 3 | | | 3 |
| Holmes (1977), (1976) | 3 | | | 3 |
| Imber and Jenkins (1981) | 3 | 1 | 144 | 148 |
| Jenkins (1980), (1986) | | 1 | 7 | 8 |
| King and Pyle (1957) | | | 2 | 2 |
| Moore (1999) | | | 2 | 2 |
| Murphy (1929) | | 2 | | 2 |
| Powlesand (1985) | 2 | | | 2 |
| Sonter (1978) | 1 | | | 1 |
| Stokes and Corben (1985) | | | 1 | 1 |
| Surman <i>et al.</i> (1997) | | | 6 | 6 |
| Taylor (2004) | 4 | | | 4 |
| Veitch (1982) | 1 | | | 1 |
| Individual observers* | | | 72 | 72 |
| Total | 124 | 31 | 1881 | 2036 |

* includes reports published online at <http://birding-aus.org>

Table 2. Timing of migration events for the two subspecies of Gould’s Petrel, as revealed by geolocators.

Dates presented as day/month; all dates from 2010. Means presented with \pm standard deviation in days.

| | | <i>P. l. leucoptera</i> | <i>P. l. caledonica</i> | <i>t</i> | <i>P</i> |
|-------------------------|-------------------|--|--|----------|----------|
| Post-breeding migration | | | | | |
| Departure | mean | 4 th April \pm 5.7 days | 25 th March \pm 29.7 days | 0.88 | 0.413 |
| | earliest – latest | 26 th March – 20 th April | 18 th February – 24 th April | | |
| | range (days) | 25 | 65 | | |
| | <i>n</i> | 22 | 7 | | |
| Arrival | mean | 24 th April \pm 9.8 days | 18 th May \pm 13.0 days | 4.57 | 0.002 |
| | earliest – latest | 7 th April – 12 th May | 4 th May – 13 th June | | |
| | range (days) | 35 | 40 | | |
| | <i>n</i> | 22 | 7 | | |
| Pre-breeding migration | | | | | |
| Departure | mean | 14 th September \pm 18.7 days | 4 th October \pm 23.5 days | 1.85 | 0.091 |
| | earliest – latest | 15 th August – 16 th October | 31 st August – 28 th October | | |
| | range (days) | 62 | 58 | | |
| | <i>n</i> | 11 | 7 | | |
| Arrival | mean | 12 th October \pm 5.5 days | 4 th November \pm 7.1 days | 7.50 | <0.001 |
| | earliest – latest | 5 th October – 26 th October | 25 th October – 16 th November | | |
| | range (days) | 21 | 22 | | |
| | <i>n</i> | 13 | 7 | | |

| | | | | | |
|--------------------|-------------------|---|--|------|--------|
| First burrow visit | mean | 18 th October \pm 5.6 days | 6 th November \pm 7.7 days | 5.56 | <0.001 |
| | earliest – latest | 11 th October – 26 th October | 25 th October – 18 th November | | |
| | range (days) | 15 | 24 | | |
| | <i>n</i> | 8 | 7 | | |

Table 3. Duration of migration and of time spent in the non-breeding range for the two subspecies of Gould's Petrel, as revealed by geolocators.

Means presented with \pm standard deviation in days.

| | | <i>P. l. leucoptera</i> | <i>P. l. caledonica</i> | <i>t</i> | <i>P</i> |
|-------------------------|--------------|-------------------------|-------------------------|----------|----------|
| Post-breeding migration | Mean (days) | 22.6 \pm 8.1 | 54.6 \pm 24.5 | 3.36 | 0.012 |
| | Range (days) | 12 – 40 | 24 – 88 | | |
| | <i>n</i> | 14 | 7 | | |
| Non-breeding range | Mean (days) | 141.3 \pm 17.6 | 135.9 \pm 31.1 | 0.42 | 0.686 |
| | Range (days) | 113 – 161 | 78 – 174 | | |
| | <i>n</i> | 9 | 7 | | |
| Pre-breeding migration | Mean (days) | 27.0 \pm 16.3 | 30.7 \pm 19.3 | 0.40 | 0.697 |
| | Range (days) | 10 – 55 | 16 – 63 | | |
| | <i>n</i> | 10 | | | |