Comparative ecology of *Pachyptila* species breeding sympatrically at Gough Island

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DECLARATION

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CONTENTS

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ABSTRACT

Prions (*Pachyptila* spp.) are one of the most abundant seabird groups of the Southern Ocean but their taxonomy, at-sea distribution and foraging ecology are poorly known. There has been considerable confusion surrounding the taxonomy of prions and their identification at sea is problematic. Recent studies have confirmed the presence of two very similar prion species breeding sympatrically, approximately three months apart, on Gough Island: *Pachyptila vittata* and *P. macgillivrayi*. This discovery raised several questions about the ecological segregation of these species. My thesis compares the breeding distribution, at-sea movements, phenology, foraging ecology and trophic segregation of the two species at Gough Island, and compares Gough birds with the *P. vittata* from Tristan da Cunha. In 2000/01 it was estimated that 1.5–2.0 million pairs of prions bred on Gough Island, suggesting that this site supports the largest populations of both species in the world. However, the contribution of each species to this total as well as spatial and temporal segregation of the two species required further investigation.

To investigate the breeding distribution and relative species proportions across Gough Island, 2227 prion specimens were collected opportunistically over several years at various sites. Most birds were caught at night or found dead, thus only provide an inference of breeding distribution. However, observations of incubating birds at several sites indicate that the data are representative of nesting distributions. At most sites there was evidence for consistent dominance of one or other species, although this need not mean local allopatry; a few *P. vittata* breed in Prion Cave, where *P. macgillivrayi* is by far the most abundant species. A few sites had both species in similar proportions, but these tended to be sites with relatively few birds and/or represent areas where the two species' ranges abut. Weighting each site equally suggested a roughly equal ratio of *P. vittata/P. macgillivrayi*, but there was little coverage of the northern and eastern glens, where *P. vittata* appears to predominate. The habitat area occupied by *P. macgillivrayi* comprises ~40% of Gough Island, suggesting they comprise ~40% of the prion population if the density of breeding birds is roughly similar for both species. Based on these proportions and the previous population estimate, some 600 000 to 1 000 000 *P. macgillivrayi* and 750 000 to 1 200 000 *P. vittata* are estimated to breed on Gough Island Additional investigation is required to elucidate the spatial segregation of the two species at a finer scale. Additional detailed categorizing of habitat types is needed to determine the fine-scale drivers for their spatial segregation.

The prions’ phenology, foraging ecology and trophic segregation was examined through geolocation technology, salt-water immersion sensors (recording time on the water), stable isotope analyses as well as a comparison of bill morphology. Breeding adults of both species were tagged with geolocators/immersion sensors on Gough Island and breeding adults of *P. vittata* were tagged at Tristan da Cunha. During their respective breeding seasons *P. vittata* largely remained within 1500 km to the north-east of the colony and *P. macgillivrayi* occupied waters within 1000 km to the south of the colony. At Gough Island, *P. vittata* departed and returned to the colony on average 91±9 days earlier than *P. macgillivrayi*. The length of the non-breeding period did not differ between species and all tracked individuals except one *P. vittata* engaged in a pre-laying exodus lasting 13-49 days. The *P. vittata* population from Tristan da Cunha departed, moulted and returned 15-17 days later than their counterparts from Gough Island. After breeding, both species showed a well-defined outward migration, with all moving west until the start of moult, except one *P. vittata* individual that moved east. Moulting was inferred from a marked reduction in the time spent in flight, which occurred shortly after arrival on the non-breeding grounds by both species (i.e. November–February for *P. vittata* and February–June for *P. macgillivrayi*). Moulting birds targeted specific areas with little overlap between species within the Argentine Basin. Both species briefly returned to their burrows after moulting. During the remainder of the non-breeding period both species were distributed more widely over the South Atlantic Ocean. Inter-specific spatial segregation was observed for most of the tracking period, especially in core use areas. *Pachyptila macgillivrayi* spent more time flying, during both daylight and darkness, than *P. vittata*. Stable isotope signatures of prion flight feathers from tracked birds and additional samples from each population indicated that movements of tracked individuals were representative of the adult population, and were similar over years. Higher δ^{15}N values found in *P. macgillivrayi* feathers is consistent with the hypothesis that *P. vittata*, being the more specialist filter feeder, targeting copepods, should forage at a lower trophic level than the more generalist *P. macgillivrayi*. This is also consistent with the greater time in flight for *P. macgillivrayi* i.e. more time actively searching for food, rather than sitting on the water filtering. Across both species, bill width was positively correlated with the number of palatal lamellae with *P. vittata* having a wider bill containing more palatal lamellae and thus better equipped for filter feeding. Habitat analysis revealed biologically meaningful, species-specific preferences for distance from the breeding colony, chlorophyll-*a* and sea surface temperature, but not distance to seamount or for water depth.

This study contributes to the growing number of studies tracking small petrels and provides information on the strategies employed by extremely similar and abundant seabirds, most notably allochrony for *P. vittata* and *P. macgillivrayi*, allowing ecological segregation as well as furthering the understanding of moult in prions. The findings of this thesis advance the knowledge of the ecology of these poorly studied species of prions.

CHAPTER 1

General Introduction

Pelagic seabirds often nest on islands that are far from productive foraging areas. This is not from choice, but from the necessity that breeding grounds have to be predator free and for large parts of the Southern Ocean, there are very few islands at which they can breed. This is especially evident in the South Atlantic, where the Tristan da Cunha group (37°S) and Gough Island (40°S) are the only islands between the Falklands (51°S) and tropical islands around 20°S (e.g. Trindade, Martim Vaz, St Helena and Ascension). This makes the four islands of the Tristan-Gough group the only breeding option for species foraging in temperate and sub-Antarctic waters in the central South Atlantic Ocean. The Procellariiformes (petrels, shearwaters, and albatrosses) are generally the longest ranging seabirds, and have several adaptations that permit them to efficiently utilize distant foraging areas, such as the ability to digest prey into an energy-rich stomach oil, energy-efficient flight, laying a single egg and having a chick that can fast for long periods (Phillips and Hamer 1999; Weimerskirch et al. 2000). As a result, these extremely remote South Atlantic islands support remarkable numbers of several seabird species, mainly comprising of procellariiformes (Ryan 2007).

This thesis examines how seabirds limit inter-specific competition allowing closely-related species to breed together at high densities. Spatial segregation is one way in which seabirds avoid competition and allow the co-occurrence of species occupying a similar niche. This concept has been exhibited by studies examining seabird colony distribution, showing an inverse relationship between colony size and distance between seabird colonies in the United Kingdom (Furness and Birkhead 1984; Lewis et al. 2001). However, this is not possible where there is a paucity of breeding sites. Another option is to segregate the timing of activities such as breeding and moulting (Friesen et al. 2007; Cherel et al. 2016; Whitehead et al. 2016; Taylor and Friesen 2017).

In the Southern Ocean, petrels (Procellariidae) are the most diverse, widespread and abundant seabird group, being only surpassed in terms of biomass by penguins (Sphenisciformes). They are an interesting group to monitor, because their behaviour and population dynamics have been shown to reflect changes in their environment (Montevecchi 1993; Monaghan 1996). This is particularly pertinent in view of significant changes happening to fisheries and climate in the Southern Ocean (Croxall 192; Perry et al. 2005). Despite this, many petrel species and populations remain poorly understood.

Prions are small (130–250 g) highly abundant planktivorous petrels which have been shown to be sensitive to changes in environmental conditions (Quillfeldt et al. 2008). These characteristics have led to suggestions that they are useful indicators of long-term changes in zooplankton communities (Quillfeldt et al. 2010). However, prion diet is linked to bill morphology (Klages and Cooper 1992; Cherel et al. 2002), so a thorough examination of their morphological diversity is needed in order to use them to infer any changes in the Southern Ocean.

The seemingly unlikely finding that two very morphologically similar species of prion (*Pachyptila*) co-existing at a single breeding site provides the basis for this thesis. Generally, prions breeding in sympatry tend to differ in bill structure, allowing them to occupy different niches by difference in diet. For example, at islands around New Zealand, Broad-billed Prions *Pachyptila vittata* (bill width: 20-24.5 mm) breed sympatrically with Fairy Prions *P. turtur* (bill width: 10-12 mm). Similarly at the Prince Edward and Crozet island groups, Salvin's Prion *P. salvini* (bill width: 14-19 mm) breed with *P. turtur*. Exceptions do occur where prions breeding in sympatry have more similar bill morphology, such as *P. salvini* and small numbers of Antarctic Prions *P. desolata* (bill width: 12-16 mm) at the Crozets, and *P. desolata* breeding with Slender-billed Prions *P. belcheri* (bill width: 9-12 mm) at the Kerguelen archipelago (Quillfeldt et al. 2015b; Cherel et al. 2016; Ryan 2017). In both of these cases there is temporal separation in the time of breeding and moult (Bretagnolle et al. 1990; Cherel et al. 2016). Thus the occurrence of *P. vittata* and MacGillivray's Prion *P. macgillivrayi* (bill width: 15.5-20.5 mm) both breeding at high density at Gough Island is unusual and begs further investigation (**Figure 1.1and 1.2**).

Figure 1.1. Breeding locations of filter-feeding prions ('whalebirds') around the Southern Ocean. Black symbols are study sites.

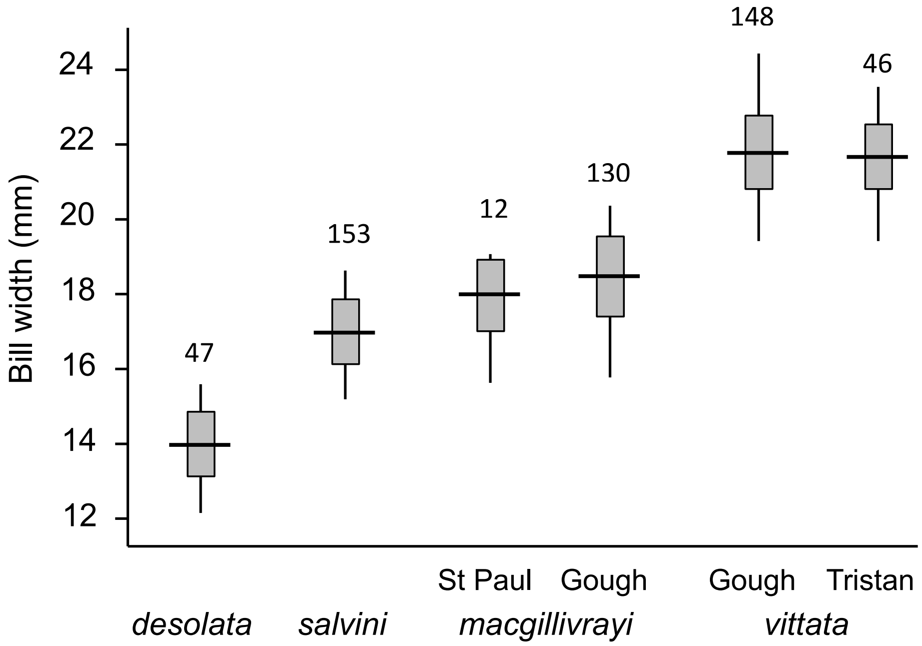

Figure 1.2. Bill widths of adult filter-feeding prions (mean ± SD, range and sample size; P.G. Ryan unpublished data).

Seabird Tracking

Procellariiformes spend most of their lives at sea, only visiting land to breed. Understanding the factors that influence their marine distribution and habitat preferences is essential for mitigating any threats they might face at sea, including the establishment of an effective, evolving network of protected areas that will safeguard against future biodiversity loss (Block et al. 2011; Frederiksen et al. 2012).

The open ocean is a dynamic environment, and pelagic predators such as procellariiformes frequently target areas of higher prey availability around areas associated with upwelling such as shelf breaks, sea mounts, and frontal systems (Wakefield et al. 2009; Kappes et al. 2010; Louzao et al. 2011a; Pinet et al. 2011). Reductions in size and improvements in battery-life and functionality of tracking devices since the 1980s have greatly enhanced our understanding of movement patterns and behaviour of marine predators (Phillips et al. 2007a). The movements of medium to small seabirds have progressively been studied with the development of global location sensor (GLS) loggers also known as geolocators (Egevang et al. 2010; Harris et al. 2010; Rayner et al. 2012; Navarro et al. 2013; 2015; Quillfeldt et al.

2013; 2015a). These devices have a large associated positional error (~200 km, Phillips et al. 2004), so are mostly used to investigate broad-scale movements. However, the light data, in combination with salt-water immersion data recorded by these devices, can detect flight patterns and periods spent on land in burrow-nesting petrels, and therefore can be used to infer various aspects of phenology (Phillips et al. 2006; Guilford et al. 2012; Rayner et al. 2012). More recently, studies that combine tracking data with remotely sensed environmental data in habitat models have provided key insights into the oceanographic factors that drive the distribution of seabirds (Péron et al. 2010; Louzao et al. 2011b; Wakefield et al. 2011; Quillfeldt et al. 2013; Grecian et al. 2016).

A limitation of many earlier biologging studies is that data are based on small sample sizes of individuals, tracked for only one season (Phillips et al. 2007a). Physical characteristics of the ocean change across space and time; distributions of prey and predator organisms are expected to vary accordingly (Pinaud et al. 2005; Žydelis et al. 2011; Quillfeldt et al. 2013). Although there is evidence from some seabirds that individuals can change their non-breeding destination (e.g. Dias et al. 2011; Grecian et al. 2016), the general trend appears to be for high regional site fidelity among migrant seabirds with evidence for high year-to-year consistency (Croxall et al. 2005; Phillips et al, 2005; 2006; Guilford et al. 2011; Thiebot et al. 2011; Yamamoto et al. 2014; Quillfeldt et al. 2014; 2015a; 2015b; Carneiro et al. 2016). It is important to note, however, that most studies represent a relatively short time period (a decade or less), when conditions may be more similar compared to longer time periods (see Grecian et al. 2016).

Intra-population variation has been observed where individuals from the same colony frequently use multiple regions or habitats during their non-breeding period (Phillips et al. 2005; Dias et al. 2011; Kopp et al. 2011). These alternative strategies may be associated with differences in age, breeding status, sex, or individual preferences (Phillips et al. 2005; Ramírez et al. 2013; Quillfeldt et al. 2015a). Migration schedules can also vary, especially in relation to sex or prior breeding outcome (Phillips et al. 2005; Bogdanova et al. 2011; Catry et al. 2013a). In addition, some non-breeding regions may be used by a small minority of individuals. For example, only 2 of 34 Black-browed Albatrosses *Thalassarche melanophris* tracked from Bird Island, South Georgia migrated to the Patagonian Shelf instead of the Benguela Upwelling Region during their non-breeding period (Phillips et al. 2005). Similarly, only 2 of 39 South Polar Skuas *Catharacta maccormicki* tracked from King George Island wintered in the Southern Hemisphere, one off Peru and the other west of Gough Island (Kopp et al. 2011). Thus, to better identify core areas for entire populations, and also to improve the accuracy of predicted distributions based on observed habitat preferences accounting for future environmental changes, tracking studies should ideally make use of a suite of biologging technologies and involve large numbers of individuals in multiple years (Hindell et al. 2003, Soanes et al. 2013).

There have been relatively few tracking studies of prions. Quillfeldt et al. (2013) showed that *P. desolata* and *P. belcheri* breeding at South Georgia and the Falklands respectively, exhibited divergent patterns of migration, which resulted in almost complete spatial segregation over their non-breeding periods. This study also produced habitat models from tracking data and found significant differences in ecological niche and habitat selection between the two species during the breeding and non-breeding seasons. Similarly, Quillfeldt et al. (2015a) tracked *P. desolata, P. belcheri* as well as Blue Petrels *Halobaena caerulea* breeding sympatrically at the Kerguelen archipelago and found that these species segregate latitudinally, with sea surface temperature being the most important variable separating the species. Habitat models from these tracking data show that *P. desolata* and *P. belcheri* from Kerguelen occupy a similar ecological niche, have similar habitat preferences and their ranges overlap slightly with their South Atlantic counterparts during the non-breeding period (Quillfeldt et al. 2015a; 2015b).

Navarro et al. (2013; 2015) investigated the co-existence during the breeding and non-breeding periods of four species of abundant, zooplanktivorous petrels from South Georgia: *H. caerulea*, *P. desolata*, and two diving petrels, *Pelecanoides urinatrix* and *P. georgicus*. During the breeding season they found that segregation was achieved through different diving depths as well as differences in spatial distribution and timing of activities, whereas spatial segregation was the main partitioning mechanism during the non-breeding period.

Cherel et al. (2016) investigated how *P. desolata, P. belcheri* and *H. caerulea* from Kerguelen adjusted their foraging ecology when they moulted their flight feathers. *Pachyptila belcheri* and *H. caerulea* moult shortly after breeding in Antarctic waters where they rely on a low trophic diet, whereas *P. desolata* moults in sub-tropical waters just before returning to the colony to breed. Grecian et al. (2016) tried to detect changes in the non-breeding distributions of *P. vittata* and *P. desolata* over the last century based on stable isotope analysis from feathers. They found that the δ^{13}C signature of *P. desolata*, but not *P. vittata*, declined during the study period suggesting a southward shift in the non-breeding distribution. The δ^{15}N signatures of both species decreased, suggesting that marine productivity has decreased over the last century. Data from geolocators indicated that *P. vittata* from Rangatira, New Zealand, begin moulting soon after their breeding season and spent their non-breeding period to the east of their breeding site where the subtropical front bisects the southern end of the Louisville seamount chain (Grecian et al. 2016). Habitat modelling revealed seamounts to be an important habitat feature for *P. vittata*, which advocated that protecting waters around seamounts may be important for reducing threats from climate driven changes in prey (Grecian et al. 2016).

Ecological Segregation of Seabirds

Habitat features govern the delivery and accessibility of trophic resources, thus are inextricably linked to the movements and behaviour of animals (Guisan and Zimmermann 2000). In the ocean, productive areas are often localized and numerous seabirds frequently target such productive areas, leading to competition for food (e.g. Ainley et al. 2009). This occurs during the breeding period, when the limited availability of suitable islands, headlands or cliffs tends to increase spatial overlap among species (e.g. Masello et al. 2010), but also in the non-breeding season, when highly mobile species, from adjacent populations, converge upon productive areas (e.g. González-Solís et al. 2007; Quillfeldt et al. 2015a).

During the non-breeding period, when not required to return to the breeding colony, many seabirds move large distances from their colonies. Most procellariiformes are migratory to some degree; the species that have been studied in detail appear to show considerable plasticity in migratory behaviour. For example, during the boreal winter, Cory’s and Scopoli’s Shearwaters *Calonectris borealis* and *C. diomedea* from North Atlantic and Mediterranean breeding colonies use three different up-welling systems of the tropical and southern Atlantic (González-Solís et al. 2007; Dias et al. 2011). Similarly, Sooty Shearwaters *Ardenna grisea* from New Zealand travel to three discrete regions in the North Pacific – off Japan, Alaska and California (Shaffer et al. 2006). Intra-population variation in the non-breeding movements of seabirds has also been suggested by carbon stable isotope ratios (Quillfeldt et al. 2008; Phillips et al. 2009).

Before geolocation, the distribution at sea of prions in particular was not well understood because species discrimination is difficult at sea due to their uniform appearance (Shirihai 2007). Some studies have tried to investigate habitat preferences from observations at sea (Ribic et al. 2011), and to determine water masses used during the non-breeding period from feather stable isotope ratios (Cherel et al. 2006; Quillfeldt et al. 2008; Phillips et al. 2009). However, the conclusions drawn from such studies are limited, given the identification difficulties at sea, and isotopic signatures only give a rough indication of latitude; neither approach provides information on specific movements. Studies using geolocators to track prions give insights into their spatial and temporal coexistence in the context of niche partitioning and community assembly rules (e.g. Quillfeldt et al. 2013). Spatial segregation often facilitates species co-existence of morphologically similar species (Chesson 2000), but given the high abundance of prions and paucity of breeding and foraging grounds, temporal and trophic segregation likely play a key role.

Morphological similarity and taxonomic challenges of prions

Until recently, six species of prions were recognized (Marchant and Higgins 1990; Brooke 2004), being identified mainly by differences in bill size and structure, but species limits within the genus are contentious, with three to seven species being posited (e.g. Cox 1980; Harper 1980; Warham 1990; Shirihai 2007). The species with wider bills, known as 'whalebirds' (*P. vittata*, *P. salvini*, *P. desolata*), possess palatal lamellae, which they use to filter-feed zooplankton (Wilson 1907; Murphy 1936; Harper 1980; Warham 1990). The number of palatal lamellae are correlated with bill width (Klages and Cooper 1992), which among the 'whalebirds' is smallest in *P. desolata* (bill width 12–16 mm) (Bretagnolle et al. 1990, Marchant and Higgins 1990). Lamellae are best developed in *P. vittata*, the species with the widest bill (20–24.5 mm, Marchant and Higgins 1990; Klages and Cooper 1992; Ryan et al. 2014), which has two distinct breeding populations (**Figures 1.1** and **1.2**): at the Tristan da Cunha archipelago (37°S) and Gough Island (40°S) in the central South Atlantic Ocean, and in the South Pacific near New Zealand – Chatham (44°S), Snares (48°S) and Stewart Island archipelagos (47°S, **Figures 1.1** and **1.2**). *Pachyptila desolata* breeds at islands mainly south of 50°S (**Figures 1.1** and **1.2**), but also in the sub-Antarctic Crozet Islands (46°), where it breeds sympatrically with *P. salvini* (bill width 14–17 mm) (Bretagnolle et al. 1990; Marchant and Higgins 1990). *Pachyptila salvini* also breeds at the Prince Edward Islands (46°S), to the west of the Crozet Islands (**Figures 1.1** and **1.2**).

There is uncertainty about the taxonomic status of the relict population of *P. macgillivrayi* now confined to St Paul Island (38°S) in the central Indian Ocean (Tollu 1984; Micol and Jouventin 2002; Jiguet et al. 2007), but formerly abundant on nearby Amsterdam Island (Worthy and Jouventin 1999). This little known form has an average bill width intermediate between *P. salvini* and *P. vittata* (see **Figure 1.2**; Roux et al. 1986), and has been regarded as a subspecies of either of these species (Harper 1980; Roux et al. 1986), as well as a distinct species (Bretagnolle et al. 1990; Worthy and Jouventin 1999; Shirihai 2007).

Working mainly with beach-washed birds, Cox (1980) recommended treating *P. vittata–salvini–desolata* as a polytypic species. However, Bretagnolle et al. (1990) indicated that adults from the three taxa have only marginal overlap in bill morphology, and at sites where they breed sympatrically, exhibit differences in phenology and nesting habitat as well as in vocalisations. *Pachyptila salvini* and *P. vittata* have been allied (Warham 1990), but some genetic data suggest that *P. salvini* is a closer relative of *P. desolata* (Nunn and Stanley 1998). Initial studies documented several subspecies of prions, mainly due to differences in morphology between populations (e.g. Murphy 1936; Falla 1940). More recently, most of these taxa were lumped, with only *P. macgillivrayi* and three subspecies of *P. desolata* being recognized (Warham 1990). *Pachyptila vittata* is usually considered to be monotypic (Marchant and Higgins 1990; Brooke 2004). Mathews (1912) suggested that birds from Tristan da Cunha and Gough Island were distinct from their New Zealand counterparts, positing the subspecies *P. v. keyteli*, but this has been refuted by more recent studies (Murphy 1936; Clancey 1981).

Until recently, *P. macgillivrayi* (Roux et al. 1986; Bretagnolle et al. 1990) was considered to be the Indian Ocean counterpart of *P. vittata* (Warham 1990). Apart from reports of some prions breeding much later than usual on Gough (Swales 1965; Cuthbert et al. 2013), there had was no indication of another prion species breeding at Gough Island until 2012, when Karen Bourgeois and Sylvan Dromzeé noted regional differences in bill width among prions on the island (Ryan et al. 2014). Subsequent observations confirmed that a population of narrower-billed prions breeds alongside *P. vittata* that are similar in bill width to *P. salvini* and *P. macgillivrayi* from the central Indian Ocean (Ryan et al. 2014). These narrower-billed birds breed roughly three months later than *P. vittata*, suggesting that they form a distinct species rather than a case of bill polymorphism (Ryan et al. 2014). Sequencing of two mitochondrial genes suggest that the narrower-billed birds on Gough Island are sister to *P.*

macgillivrayi, with both more closely related to *P. vittata* than *P. salvini* (which is sister to *P. desolata*; **Figure 1.3**, P.G. Ryan unpublished data). The similarity in morphology and genetics between the narrow-billed birds found at Gough Island and *P. macgillivrayi* supports grouping them as the same species (cf. Tobias et al. 2010; P.G. Ryan unpublished data).

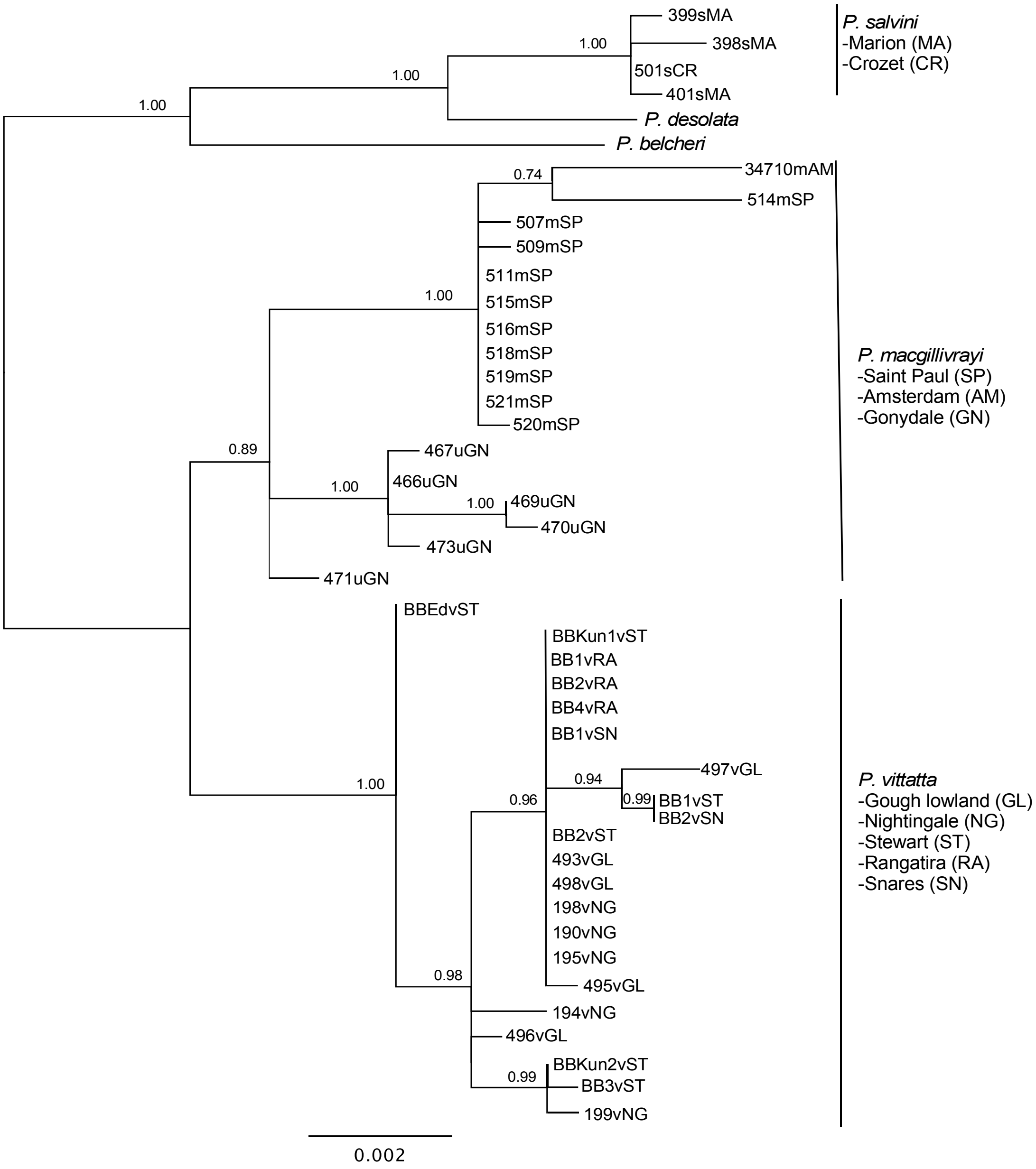

Figure 1.3. Phylogenetic relationships among prion taxa (n=44 sequences) inferred using a partitioned Bayesian analysis based on cyt *b* and COI sequences (P.G. Ryan unpublished data).

The conservation status of *P. macgillivrayi* was only assessed for the IUCN Redlist in 2016, because prior to recent findings it was not recognised as a species by BirdLife International. The Indian Ocean population is very small, with an estimated 150-200 pairs mostly confined to La Roche Quille, a rock stack 150 m off the coast of St Paul Island (Tollu, 1984; Jiguet et al. 2007). The species was once abundant on Amsterdam Island and St Paul, but was extirpated from both islands by introduced predators (Worthy and Jouventin 1999; Jiguet et al. 2007). Small numbers of prions have recolonised St Paul from La Roche Quille following the eradication of Black Rats *Rattus rattus* from St Paul in 1997 and European Rabbits *Oryctolagus cuniculus* in 1999 (Micol and Jouventin 2002; Griffiths 2011). Unfortunately, House Mice *Mus musculus* remain on St Paul Island (Micol and Jouventin 2002), and predation by mice may slow or even halt the recovery of prions (see Dilley et al. 2015). This population is also at risk from vagrant falcons that occasionally reach the island (Jiguet et al. 2007).

The population size of Macgillivray's Prion on Gough Island is not well known, but based on previous estimates of their proportions in skua middens, they comprise at least 20% of prions breeding on the island (P.G. Ryan unpublished data). Cuthbert (2004) estimated there were 1.5-2.0 million pairs of prions breeding on Gough Island in 2000/01. This estimate might be somewhat inflated because it was based on burrow counts in lowland areas only, and numbers of prions have probably decreased since, due to predation on their eggs and chicks by invasive house mice (Cuthbert et al. 2013; Dilley et al. 2015), but the most recent estimate suggests that Gough Island supports at least 100 000 pairs of Macgillivray's Prions (BirdLife International 2017). This site is thus home to more than 99% of the species' global population. Macgillivray's Prion qualifies as Endangered under IUCN Redlist Criterion B2a (two populations with a total breeding area <70 km^2) and B2b because the species has experienced very poor breeding success (0-15%) at Gough Island in recent years due to mouse predation (Dilley et al. 2015).

Objectives and Aims

This thesis examines how the two prions breeding on Gough Island are distributed throughout the island (Chapter 2), as well as their movement, flight patterns and habitat preference at sea (Chapter 3) during discrete stages of their yearly cycle. In Chapter 2, I evaluate data from skulls collected over several seasons from various locations around Gough Island to infer the breeding distribution of the two species. Ryan et al. (2014) found strong spatial separation in the south-eastern sector of Gough Island, despite the marked temporal separation in time of breeding. The reason for this spatial segregation is unclear, and I test whether the spatial segregation is consistent over time, and whether it occurs throughout the island. If the spatial segregation is consistent over time, then an estimate can be made of the relative contribution of each species to the island population. I discuss possible reasons for the separation in breeding habitat and make recommendations for future sampling efforts, with reference to the need for a more comprehensive population update and detailed categorizing of nesting habitat preferences.

In Chapter 3, I describe at-sea movements, activity patterns and habitat preference during discrete periods in the annual cycle of prions breeding on Gough Island and Tristan da Cunha. I test whether *P. vittata*, which is expected to have a more specialist diet given its broader bill, should occupy a lower trophic level mainly in subtropical waters (Grecian et al. 2016) and whether *P. macgillivrayi* at least partially segregates from *P. vittata*, perhaps by travelling farther distances in pursuit of a more general dietary items rather than sitting on the water filter-feeding. This prediction is based on the finding that the number of palatal lamellae in prions is a good proxy of diet, and numbers of lamellae are correlated to bill width (Klages and Cooper 1992). Observations of breeding phenology suggest that the annual cycles of the two populations on Gough are roughly three months apart, which means they are faced with different conditions during their respective breeding and non-breeding periods. Spatial separation is also expected because each species will have their own respective limitations in movements during the same time interval i.e. when *P. macgillivrayi* are restricted to waters around Gough Island during their breeding season, *P. vittata* are free to migrate since they are finished breeding at this time. Similarly, the energetically costly moult period is staggered. I test whether they use the same moult areas. Overall I expect to detect differences in activity patterns and habitat preferences, and the results are discussed in the context of ecological niche specialization (Navarro et al. 2013; 2015; Quillfeldt et al. 2013; 2015a; 2015b; Cherel et al. 2016).

The thesis provides the first tracking information of these two species of prion breeding on Gough Island and adds to a growing number of studies tracking small petrels to further understand their movements in relation to environmental change (Quillfeldt et al. 2010; Cherel et al. 2014; Grecian et al. 2016). In addition, this thesis adds valuable knowledge about the population dynamics of these difficult to census burrowing species that have recently been shown to be at risk of several conservation threats.

Chapter 2

Nesting distribution and relative proportions of two *Pachyptila* species breeding sympatrically on Gough Island

ABSTRACT

Genetic data has recently confirmed that two species of prion, Broad-billed *Pachyptila vittata* and MacGillivray's *P. macgillivrayi*, breed sympatrically, but roughly three months apart on Gough Island, central South Atlantic Ocean. Initial observations, confined to the south-eastern third of the island, indicated that these two species appear to be largely allopatric at a local scale. Thus this study aims to ascertain the island-wide distribution and the relative proportion of each species. Large numbers of prion specimens were collected opportunistically over several years at various sites around Gough Island. These species are similar in morphology but can be differentiated by bill width, averaging 21.8±0.98 mm (±SD, n=143) for *P. vittata* and 18.5 ± 1.09 mm (±SD, n=131) for *P. macgillivrayi*. However, there is an overlap in bill morphology as bill width falling beyond 95% probability of species limits could not confidently be assigned to one species or the other. Cautiously, bills falling within the 20 – 20.5 mm range were excluded and reported as uncertain. There is clear evidence for spatial segregation with local scale allopatry evident island-wide and most sampling sites showed a dominant prevalence of one species or the other with remarkable consistency over time. A few sites had both species, either because both bred in the area or because the sampling area straddled species borders. Such areas tended to have low densities of prions (as evidenced by the small number of samples collected). By weighting each site equally and in relation to approximate habitat area, *P. macgillivrayi* was estimated to comprise 40-50% of prions on Gough, meaning the proportion of this new discovered population is likely more significant than the previous estimate of 20%. Based on these proportions and the previous population estimate, some 600 000 to 1 000 000 *P. macgillivrayi* and 750 000 to 1 200 000 *P. vittata* are estimated to breed on Gough Island. Further research is needed to better understand the breeding distribution of the two prion species on Gough Island as this study only infers broad patterns from remains of prions killed by Brown Skuas *Stercorarius antarcticus*. Additional detailed categorizing of habitat types should be done in order to begin to understand the drivers for local scale allopatry.

INTRODUCTION

Competition for nest sites between seabird species at breeding colonies results from an overlap in habitat requirements (Whittam and Siegal-Causay 1981; Ramos et al. 1997), unless there is complete segregation in the timing of breeding. Thus similar species with an overlap in phenology should exhibit clear spatial segregation in nesting distribution (Burger and Gochfield 1988). Meaning such species should have preferences for specific physical features of a habitat at breeding colonies (e.g. Ramos et al. 1997). Thus, the stability and breeding success of seabird populations is reliant on the accessibility of appropriate nesting habitat (Storey and Lien 1985; Newton 1998). There is a paucity of breeding sites for seabirds in the Southern Ocean, consequently, there is likely inter- and intraspecific competition for suitable nest sites, which has shaped how species breeding on remote islands adapt in terms of their nesting habitat requirements (Lack 1968; Burger and Gochfield 1988). Considering this, one would expect more flexible species (i.e. generalist in habitat preference) to be more abundant than species more rigid in their habitat requirements (Lack 1968).

Since burrow-nesting Procellariiformes are the most abundant group of birds in the Southern Ocean, they are interesting candidates when investigating nesting distributions and habitat requirements at breeding colonies (Ramos et al. 1997). Gough Island is one of very few breeding sites for seabirds in the South Atlantic, due to this there has likely been competition for potential nesting sites among prions especially before the introduction of invasive House Mice *Mus musculus*, when population density would have been higher (Dilley et al. 2015). As a result of high population density and limited nesting space, these birds seem to have a broad nest-site preference and are found in a diversity of habitat types. (Ryan 2007; Ryan et al. 2014).

Recent genetic studies of two prion morphs on Gough Island (Ryan et al. 2014), suggest that they are two monophyletic clades that are best treated as separate species: Broad-billed *Pachyptila vittata,* and MacGillivray's *P. macgillivrayi* prions breeding sympatrically on Gough Island (BirdLife International 2017). Although *P. vittata* is considered not-threatened, *P. macgillivrayi* has recently been listed as Endangered (BirdLife International 2017). Population size, trends or ecology of either species is poorly understood at Gough Island as no recent censuses have been done (Ryan et al. 2014). Swales (1965) loosely estimated that there were approximately 10 million pairs of prions breeding on Gough Island in the 1950s, however prion numbers have probably since declined because of intense predation by invasive House Mice *Mus musculus* (Cuthbert et al. 2013; Dilley et al. 2015). Cuthbert (2004) updated the estimate to approximately 1.5–2.0 million pairs of prions at the island in 2000/2001. Even allowing for ongoing decreases over the last two decades, Gough Island still supports the largest breeding populations of both species (Brooke 2004), and is the only site where these species breed sympatrically (Ryan et al. 2014; BirdLife International 2017).

Nesting habitat preferences of prions on Gough Island have not been quantified. Ryan et al. (2014) reported that the two species of prion on Gough Island appeared to be allopatric at local scale in the southeast third of the island. This chapter reports on the spatial distribution over a more extensive coverage of Gough Island over several seasons and attempts to answer and discuss some of the important questions posed by Ryan et al. (2014). Specifically: what is the distribution of prion taxa on the island is this consistent over successive years, how much spatial overlap occurs between species across the island and are there any species-specific habitat preferences? These data are then used to estimate the approximate proportions of prion taxa on Gough Island. An improved understanding of nesting distribution and the proportion that each species contributes to the previous population estimate (Cuthbert et al. 2004) will aid the conservation of these taxa.

METHODS

Study site

Fieldwork for this thesis was conducted at the Tristan da Cunha archipelago situated in the central South Atlantic Ocean. The Tristan group are the only oceanic islands in the Atlantic Ocean between 20° and 50°S. The fieldwork for this chapter was conducted at Gough Island (40.32°S; 9.94°W), the most remote island in the Tristan group, approximately 400 km southeast of the main island, Tristan da Cunha (37.07°S; 12.32°W) (**Figure 1.1; 2.1**). It is an inactive volcanic island of roughly 65 km^2 that rises up to 900 m above sea level at its highest point.

Fieldwork

This study includes data from samples collected during fieldwork conducted from September 2014 to September 2017 at Gough Island. Sampling was done in order to gain an understanding of the occurrence and distribution of both species throughout the whole island.

Live prions were caught at night, by dazzling them with a spotlight, at several sites, as well as during the day from burrows at some sites, but mostly from Prion Cave, an accessible cave that supports many breeding prions (Klages and Cooper 1992; Cuthbert et al. 2013). However, most samples were from the remains of dead prions. Gough Island supports a large population of Brown Skuas *Stercorarius antarcticus* that feed extensively on prions. Prey remains in skua middens provide a convenient method to sample large numbers of prions across the island. Specimens were collected at locations from around most of the island readily accessible on foot (**Figure 2.1**).

Material from 2014 to 2017 was collected from 18 sites (**Figure 2.1**): Seven sites encompass low to mid elevation (30-250 m above sea level) which comprises tussock grassland and fern bush vegetation (Ryan 2007): the area around the meteorological station (hereafter termed ‘base’, elevation 30-50 m), Admirals (north of the base, 30-50 m), around South Point (from Cavern Head to Rockhopper Point, 30-200 m) and in Prion Cave (50 m), Golden Highway (200-250 m), along the path to Gonydale (mainly adjacent to a series of prion breeding caves, 200-250 m) and an area on the eastern side of the island at an area known as Serengeti (30-250 m). The other 11 sites were in short, upland wet heath vegetation at high elevation, between 400-600 m: Gonydale Hummocks, Tafelkop, Triple Peak, Tarn Moss, Low Hump, False Peak, Sea Hen Crag, GP Valley, West Point, Spire Crag, and Green Hill. The bias in coverage towards high elevation sites is a result of the island’s topography, with most of the coastline consisting of steep cliffs incised by deep valleys, making most low/mid elevation localities away from the southern part of the island challenging to access on foot.

Material from 2014 to 2017 was augmented by data from Ryan et al. (2014), which examined samples from six sites in the southeastern sector of Gough Island (**Figure 2.1**): Base, Prion Cave, South Point, Golden Highway, Gonydale path and Gonydale hummocks. Most birds examined by Ryan et al. (2014) had been fresh carcasses killed by skuas, but also included live birds caught at night, and from Prion Cave. Data collected in 1984 from 73 fresh carcasses were included from Klages and Cooper (1992). Only a few fresh carcasses could be sexed, but comparison between sexes was not included in this study as prions are monomorphic and there is no difference in bill size between sexes (Ryan et al. 2014).

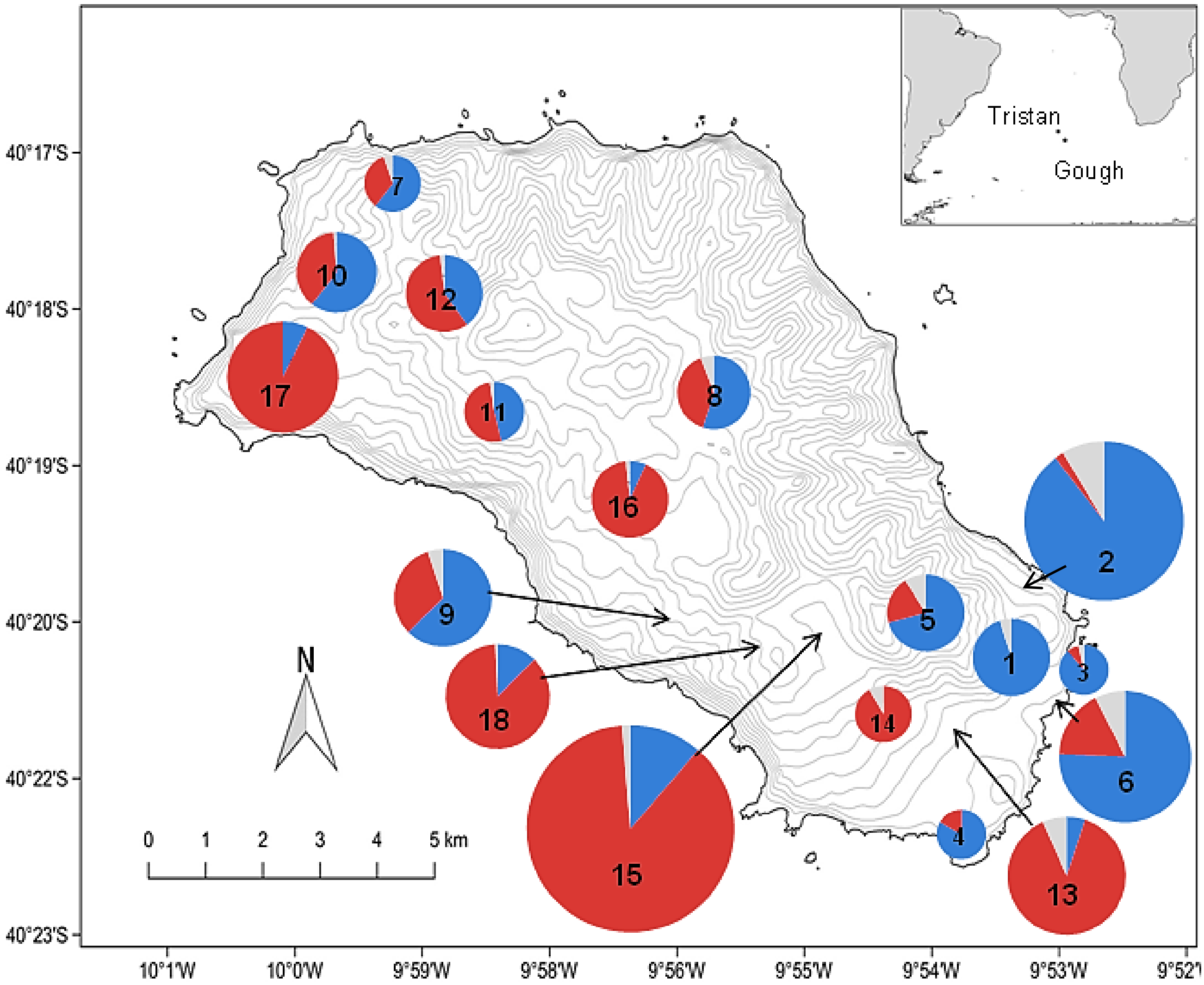

Figure 2.1 Gough Island, showing the 18 sampling locations. Site labels have been ordered by descending mean bill width. Pie charts represent the relative proportion of each species within sampling sites, scaled to sample size. *Pachyptila vittata* are shown in blue, *P. macgillivrayi* shown in red, uncertainty shown in grey. 1. Golden Highway (n=60), 2. Serengeti (326), 3. Admirals (27), 4. South Point (24), 5. Tafelkop (55), 6. Base (255), 7. Triple Peak (38), 8. Tarn Moss (51), 9. Low Hump (99), 10. GP Valley (71), 11. False Peak (41), 12. Seahen Crag (55), 13. Prion Cave (201), 14. Gonydale path (36), 15. Gonydale (523), 16. Spire Crag (59), 17. West Point (191) and 18. Green Hill (129).

Maximum bill width was measured with Vernier callipers to the nearest 0.1 mm. Other measurements that were taken are excluded from further analysis as bill width is the best predictor of species limits in this complex (Ryan et al. 2014). Throughout the course of the fieldwork several observers carried out measurements, but the comparability of measurements was ensured by training all observers until they measured the same set of specimens to within ±0.1 mm. 90% of measurements were done by either myself or my supervisor, thus less than 10% of measurements differed by more than10%.

Specimens collected in lowland areas tended to be fairly fresh, possibly because Gough Moorhens *Gallinula comeri* scavenge the remains, and/or because the dense vegetation at low/mid elevation makes old specimens harder to find. However, in the upland areas, where the vegetation is much shorter and moorhens are absent, most remains are skulls lacking the horny rhamphotheca and the underlying flesh. A correction factor was generated to correct for the narrower bill width of skulls lacking the horny rhamphotheca. Bill widths were measured from a sample of fresh specimens and then wet soaked in order to remove the rhamphotheca entirely and re-measured. These specimens consisted mainly of *P. vitatta* (but included two samples of *P. macgillivrayi*) and *P. salvini* collected during September 2017 from Gough and Marion Island (46.87°S; 37.85°E), respectively. *Pachyptila salvini* were included due to the scarcity of fresh *P. macgillivrayi* specimens available at that time and in order to test whether bill width influenced the correction factor.

Data Analysis

Prion samples were grouped geographically, with site boundaries being decided by landscape features, such as major ridges and mountain peaks. Fine-scale spatial resolution of samples was not done because most samples were prey remains usually found near skua middens and thus only representative of the coarse-scale distribution of prions in the vicinity of skua territories (see Ryan et al. 2014). Sites were sampled opportunistically and not systematically, leading to different sample sizes per site, thus do not reflect difference in abundance of species in different areas. However, there are clear concentrations of prion remains in some areas, typically where there are cave-like crevices (e.g. Gonydale and West Point). By comparison, prion remains are scarce in flat areas, particularly where mires are the dominant vegetation type. In order to encompass a plausible range of values, the relative species ratio was inferred by equally weighting each sampling site. However, this fails to address the poor coverage of lower elevation areas throughout much of the island's periphery. Given some evidence of altitudinal differences in the abundance of the two species, I also estimated the species ratios for fernbush and higher elevation wet heath habitats separately, and then under the assumption of equal density across habitats, I extrapolated these ratios according to the area of each habitat on the island. Habitat areas were estimated using Google Earth Pro v7.3.1.4507 (Google LLC, Googleplex, Mountain View, California) to determine the total area of the broad vegetation types utilized by each species.

The correction factor to predict fresh bill width from skulls was estimated using a linear regression with best fit line and 95% confidence limits. Univariate tests were used to examine differences within and among sites. This approach was preferred over multivariate comparisons because they emphasized disparity in bill width, and because it will assist species identification in the field from standard morphometric measurements (Ryan et al. 2014). In order to quantify the relative proportion of species in sampling sites, a cut-off measurement of bill width separating species needed to be decided. There appears to be some degree of overlap between the two species; Ryan et al. (2014) found the average bill width to be 21.8±0.98 mm (n=143) for *P. vittata* and 18.5±1.09 mm (n=131) for *P. macgillivrayi*. Assuming that bill widths falling beyond the 95% probability of species limits (1-tailed test = 1.65×SD from the mean), bills 20.2–20.4 mm wide could not confidently be assigned to either species. To be conservative, bill widths from 20–20.5 mm were reported as uncertain.

RESULTS

Bill width correction factor

The absolute difference between bill widths with and without rhamphotheca was significantly less in *P. salvini* (1.05±0.07 mm, n=15) than *P. vittata*/*P. macgillivrayi* (1.39±0.31 mm, n=28; t_{24} = -2.19, p=0.008). However, the proportional difference (i.e. measured difference relative to bill width) did not differ significantly between these species (t_{21} = -0.241, p=0.812). This suggests that the thickness of the rhamphotheca decreases with decreasing bill width but proportionately to the width of the bill. Considering this and the close match in slope of regression lines fitted to each species (**Figure 2.2**), there does not appear to be an effect on rhamphotheca thickness in relation to bill width in prions. Thus the data from both species were combined in order to strengthen the prediction of the regression model for correction. The regression between bill width with and without rhamphotheca was strong (**Figure 2.2**), explaining 98.6% of the variance (r^2=0.986).

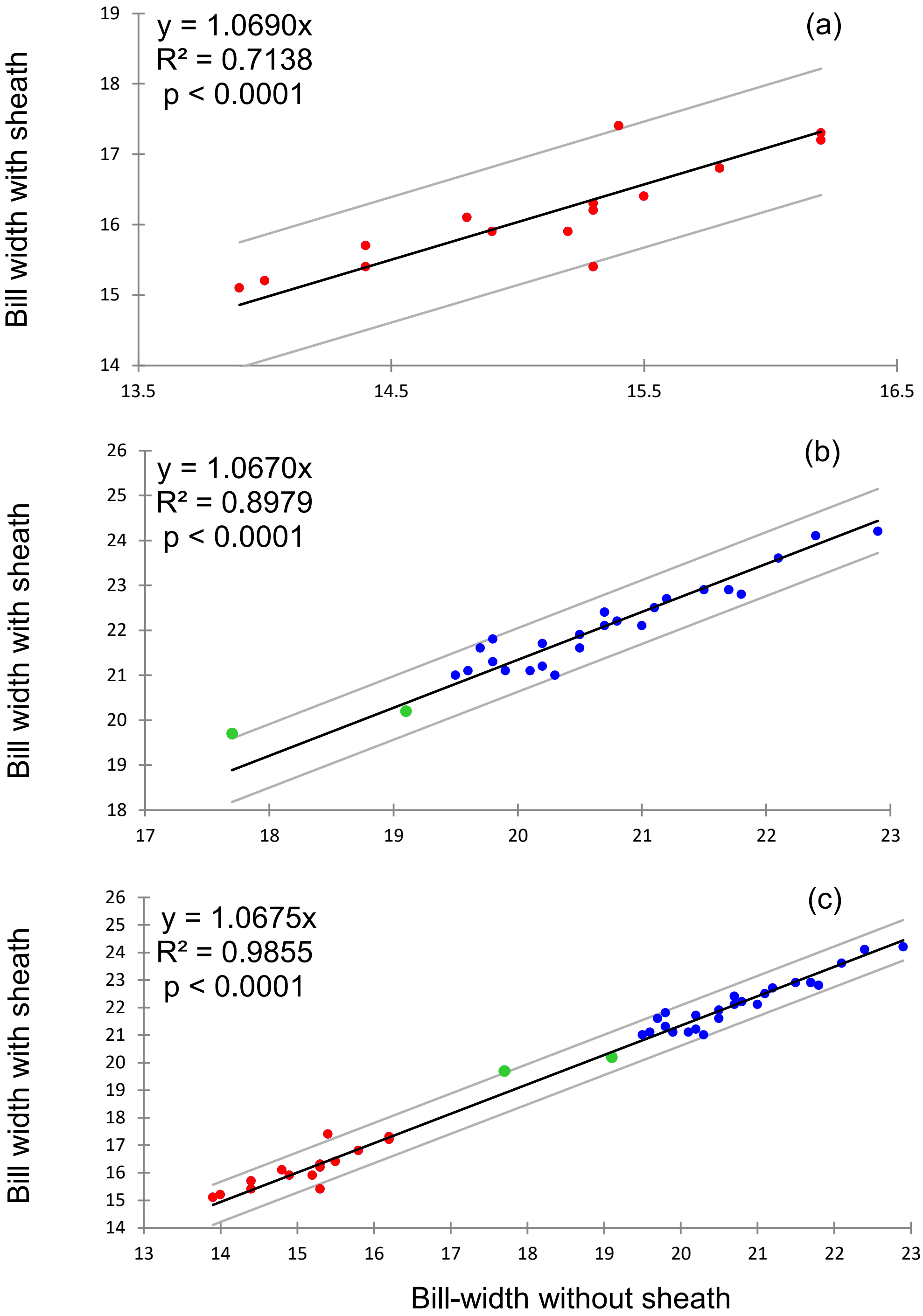

Figure 2.2. Comparison of the relationships between bill width (mm) with and without rhamphotheca after wet soaking. (a) *Pachyptila salvini* (red), (b) *P. vittata* (blue), *P. macgillivrayi* (green), (c) combined. Regression parameters are given along with 95% prediction limits (grey lines), coefficients of determination (R^2) and level of statistical significance (p).

Temporal Consistency

Since sampling was conducted at different times of the year and over several years, temporal consistency needed to be ascertained before any spatial analyses of the dataset. Across the 18 sampling sites, 2227 specimens were measured: 223 live birds, 630 fresh carcasses and 1374 skulls. Fourteen of the 18 sites were sampled on more than one occasion (**Table 2.1**). Although there are collections from different times of the year, most samples were collected in September each year from 2014 to 2017 (**Table 2.1**). This coincides with the start of the *S. antarcticus* and *P. vittata* breeding season, which could potentially lead to a bias in the species ratio among skua prey remains. However, most samples were old skulls (especially in the highlands), so the date of death (i.e. when the live prion was on the island) was not known, and likely dated back to the previous breeding season. Almost all sites that had sample sizes >50 birds and a normal distribution in bill sizes showed remarkable consistency in mean and median bill width, not exhibiting any significant change over several years. Of these sites, only the Gonydale path showed any significant change over time, but most specimens collected at this site still fell within the *P. macgillivrayi* species limits. Three sites, Tarn Moss, GP Valley and Low Hump, had a bimodal bill width distribution, presumably because they straddled the boundary between the two species' ranges. They showed some inconsistency over time, linked to the modest sample sizes and patchy distribution of the two prions within these sites. The consistency over several years for most sampling sites argues against any serious biases caused by sampling at different times of the year, and suggests that in most cases the sample collections are representative of the dominant prion species within a site. As a result, samples within sites were combined across years, and further analysis focused on spatial comparisons.

Table 2.1. Comparison of bill widths over time within sites. Values are means ± SD, with sample size in brackets. Values not sharing the same superscript letter are significantly different at the 0.05 level (ANOVA, Newman–Keuls range tests for sites with a normal distribution and Kruskal-Wallis test for bimodal sites).

	Sep-13	Sep-14	Nov-14	Dec-14	Feb-15	Mar-15	May-15	Sep-15	Sep-17	Statistics
Golden Highway	21.8 ±0.8 (10)	22.1 ±0.9 (15)	/	/	/	/	/	/	21.8 ±0.8 (35)	$F_{(2, 57)} = 0.78, p = 0.47$
Serengeti	/	22.1 ±1.0 (66)	22.0 ±0.7 (18)	/	/	/	/	21.1 ±1.6 (3)	21.7 ±0.9 (239)	$F_{(3, 322)} = 4.23, p = 0.24$
South Point	22.0 ±1.3 (10)	21.6 ±1.0 (8)	/	/	/	/	/	/	20.7 ±1.4 (6)	$F_{(2, 21)} = 2.04, p = 0.16$
Takelkop	/	19.9 ±2.7 (6)	/	22.0 ±0.8 (11)	21.0 ±0.8 (18)	/	/	21.4 ±1.3 (20)	/	$F_{(3, 51)} = 3.83, p = 0.05$
Base	21.3 ±1.7 (133)	/	/	/	/	21.5 ±1.3 (50)	/	/	21.2±1.8 (58)	$F_{(2, 238)} = 1.81, p = 0.17$
Tarn Moss	/	19.2 ±2.1 (13)^{a}	/	/	21.1 ±1.7 (37)^{b}	/	/	/	/	$K_{(1, 50)} = 8.99, p < 0.01$
Low Hump	/	21.3 ±1.7 (41)^{a}	/	/	/	20.1 ±2.3 (29)^{ab}	/	18.4 ±1.3 (10)^{b}	20.4 ±1.8 (19)^{b}	$K_{(3, 99)} = 14.87, p < 0.01$
GP Valley	/	/	/	/	19.8 ±1.8 (26)^{a}	/	/	18.1 ±0.8 (7)^{b}	21.1 ±2.1 (38)^{a}	$K_{(2, 71)} = 15.94, p < 0.01$
Prion Cave	19.1 ±1.0 (55)	19.0 ±0.7 (20)	19.0 ±0.7 (76)	18.5. ±0.7 (28)	18.5. ±0.8 (20)	/	/	/	/	$F_{(5, 197)} = 5.04, p = 0.47$
Gonydale path	/	18.7 ±0.7 (28)^{a}	/	/	/	/	/	/	17.6 ±0.9 (8)^{b}	$t_{34} = 4.72, p < 0.01$
Gonydale	17.9 ±1.3 (51)	/	/	/	18.6 ±1.8 (42)	18.5 ±1.6 (70)	18.1 ±1.3 (58)	18.7 ±1.9 (56)	18.0 ±1.6 (246)	$F_{(5, 517)} = 3.36, p = 0.57$
Spire Crag	/	17.9 ±0.8 (10)	/	/	18.1 ±1.4 (43)	/	/	18.9 ±2.7 (3)	18.4 ±1.7 (3)	$F_{(3, 54)} = 0.36, p = 0.87$
West Point	/	18.0 ±1.3 (60)	/	/	18.3 ±1.8 (48)	/	/	17.7 ±1.5 (4)	17.8 ±1.3 (79)	$F_{(3, 187)} = 1.43, p = 0.235$
Green Hill	/	17.8 ±1.7 (83)	/	/	/	/	/	/	18.0 ±1.6 (46)	$t_{127} = 3.36, p < 0.01$

Spatial Comparison and Species Proportion

The combined data set had a strongly bimodal distribution in bill width, resembling two normal distributions with an overlap at species margins (20-20.5 mm; **Figure 2.3**). Pooling birds from different sites into two groups on the basis of the predominant bill size per site indicates definite site-specific species prevalence. Prions from the base, the Golden Highway, Serengeti, Admirals, Tafelkop and around South Point were not significantly different (ANOVA, $F_{5,727}$=4.9, p=0.37), with all six sites being strongly dominated by *P. vittata* (**Table 2.2**, **Figure 2.1**). Similarly, sites that were strongly dominated by *P. macgillivrayi* (i.e. Prion Cave, Gonydale Path, Gonydale, West Point, Spire Crag and Green Hill) also show no significant difference in bill width (ANOVA, $F_{5,1133}$=13.3, p=0.25). However, both groups are faintly bimodal (**Figure 2.3**), possibly because of leakage from neighbouring sites or a small degree of local sympatry (also see 'Discussion'). Overall, these data suggest a weak tendency for east-west segregation, with *P. vittata* dominating the east.

However, six sites: Triple Peak, Tarn Moss, Low Hump, False Peak, Sea Hen Crag, and GP Valley, do not strongly conform to one species strongly dominating over the other i.e. where species proportion is closer to parity and there is strong bimodal distribution within sites (**Figure 2.3**). This result is likely due to these sites straddling a species border, encompassing multiple habitat types or leakage from a neighbouring high density species-specific site. For example, at the Low Hump site, birds on the more open areas at higher elevation are mostly *P. macgillivrayi*, whereas lower down, where vegetation changes to fernbush habitat, they are mostly *P. vittata*. Similarly, sites like GP Valley, Triple Peak and Tarn Moss appear to be weakly dominated by *P. vittata* (>55% of specimens), but exhibit low density, whereas *P. macgillivrayi* are abundant at adjacent sites such as West Point and Spire Crag, and there is likely some spill over into adjacent low density *P. vittata* areas.

When the 4.1% of samples that could not be confidently assigned to a species (bills of 20-20.5 mm) were removed, the combined dataset produces a *P. vittata: P. macgillivrayi* ratio of 918:1217 (43:57). However this is not representative of the total island population, because sampling effort varied among sites, and more importantly, there was a bias toward higher elevations, with much of the north and east coast not sampled at all (**Figure 2.1**). If sites are equally weighted the average species ratio is 51:49. This suggests each species occurs at roughly equal abundance across the whole island. Areas, identified from sampling sites, dominated by *P. macgillivrayi* and *P. vittata* were estimated to comprise about 27 km^2 and 38 km^2, respectively (41.5% and 58.5% of the 65 km^2 island area, based on areas estimated using Google Earth Pro). If sampling site ratios are estimated in relation to ratios from sample collection and broad species habitat area, *P. macgillivrayi* and *P. vittata* are estimated to comprise 40-50%% and 50-60% of the prions on Gough Island, respectively. Using these proportions in relation to the previous crude population estimate by Cuthbert (2003) of 1.5- 2 million breeding pairs, there are 600 000–1 000 000 pairs of *P. macgillivrayi* and 750 000–1 200 000 pairs of *P. vittata* breeding on Gough Island.

Table 2.2. Bill widths (mm) of prion specimens collected from September 2013 to September 2017 at 18 sites on Gough Island. Specimens consisted of live birds, freshly dead birds and skulls. Skull measurements were corrected to account for the lack of a rhamphotheca (see **Figure. 2.2**). Relative proportion of *P. vittata* (BBP), *P. macgillivrayi* (MP) and undefined samples within sites are expressed as percentages.

Site	Mean (±SD)	Min	Max	n	% BBP	% MP	% undefined	Habitat
Golden Highway	21.9 (±0.9)	20.2	24.0	60	95	0	5	Fernbush
Serengeti	21.8 (±0.9)	19.1	24.2	326	90	2	9	Fernbush
Admirals	21.7 (±1.3)	18.1	24.4	27	89	7	4	Fernbush
South Point	21.5 (±1.3)	18.5	23.2	24	83	17	0	Fernbush
Tafelkop	21.3 (±1.5)	15.6	23.4	55	71	20	9	Wet heath
Base	21.3 (±1.7)	15.2	24.4	255	76	17	7	Fernbush
Triple Peak	20.8 (±2.0)	17.3	23.8	38	61	34	5	Wet heath
Tarn Moss	20.6 (±2.0)	17.1	24.1	51	55	39	6	Wet heath
Low Hump	20.5 (±2.1)	15.1	23.9	99	63	32	5	Wet heath
GP Valley	20.3 (±2.1)	16.0	23.4	71	61	38	1	Wet heath
False Peak	20.2 (±1.7)	17.2	23.3	41	46	51	2	Wet heath
Sea Hen Crag	20.0 (±2.3)	14.7	24.3	55	40	58	2	Wet heath
Prion Cave	19.0 (±0.8)	17.0	23.0	201	4	89	6	Fernbush
Gonydale path	18.4 (±0.9)	16.2	20.2	36	0	92	8	Fernbush
Gonydale	18.2 (±1.6)	15.8	23.7	523	11	88	1	Wet heath
Spire Crag	18.1 (±1.4)	16.2	23.2	59	7	92	2	Wet heath
West Point	18.0 (±1.5)	15.5	23.6	191	7	93	0	Wet heath
Green Hill	17.8 (±1.6)	15.8	23.6	129	12	87	1	Wet heath

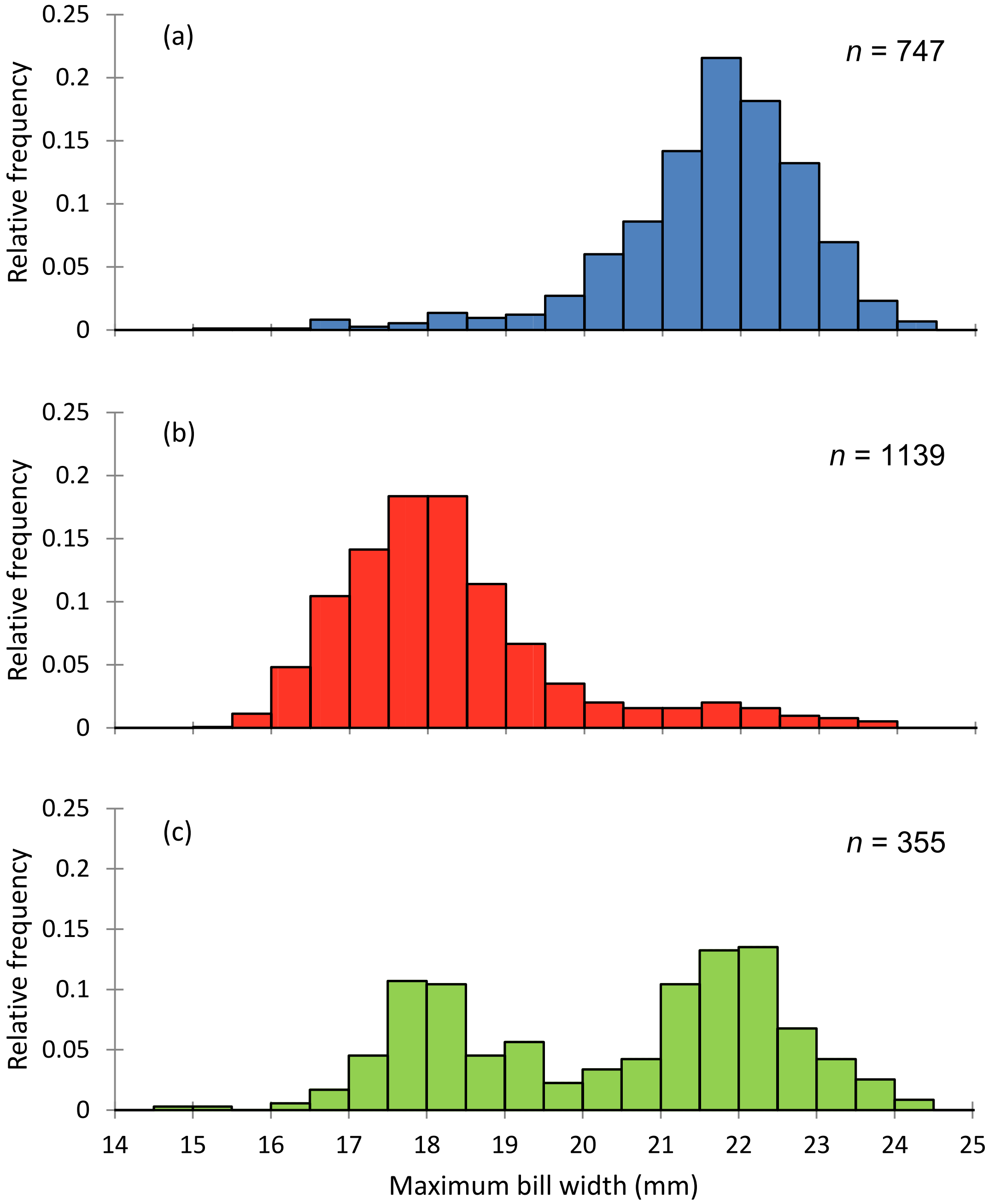

Figure 2.3. The frequency of bill widths among sites pooled on the basis of predominant bill width. (a) Golden Highway, Serengeti, Admirals, South Point, Tafelkop, Base (blue, *P. vittata* dominant sites) compared with birds grouped from (b) Prion Cave, Gonydale path, Gonydale, Spire Crag, West Point, Green Hill (red, *P. macgillivrayi* dominant sites) and (c) Triple Peak, Tarn Moss, Low Hump, GP Valley, False Peak, Sea Hen Crag (green, mixed sites).

DISCUSSION

The strongly bimodal frequency distribution of prion bill widths across sampling sites on Gough Island supports previous reports that the two species exhibit allopatry at a local scale (Ryan et al. 2014). The data from repeated sampling sites over several years confirm that this pattern of spatial segregation is consistent over time. Prion fledglings have narrower bills on average than adults (Harper 1980), but differences in average bill width between adult and fledgling are modest (~1.3 mm, Richdale 1965; Marchant and Higgins 1990). Although some samples on Gough Island were collected when fledglings leave their nests, most were collected at other times and probably represent fully grown birds. The difference in bill morphology between species on Gough Island (average 3.8 mm difference in bill width) is comparable to prion species breeding sympatrically at Ile de l'Est in the Crozet archipelago (Bretagnolle et al. 1990). Ryan et al. (2014) alluded to a possible third bill morph that falls within the morphological range of *P. salvini* but there are insufficient new data to explore this pattern; further investigation is needed to understand this phenomenon. Overall, the data demonstrate the two prion species exhibit allopatric breeding on an island-wide scale. Birds conforming to typical *P. vittata* (bill width >20.5 mm) predominate along the south and east coasts and adjacent slopes of South Peak. *Pachyptila macgillivrayi* (<20 mm) predominate in caves from near sea level to at least 450 m and appear to be more prevalent along the north and west coasts. Interestingly there appears to be some zones of overlap where one species does not seem to dominate over the other. Given the extent of temporal difference in breeding chronology and low breeding success of both species (Dilley et al. 2015), some spatial overlap is unsurprising. However it is difficult to tease apart a pattern of the occurrence of overlap within sites as distributions appear patchy. It is likely that these bimodal sampling sites either straddle a border of species specific zones or contain leakages from neighbouring sites that are strongly dominated by one species in abundance (see results).

There is a paucity of data on actual breeding distribution and this study only infers this as the dataset mostly comprises of carcasses from skua prey remains. This study probably underestimates the degree of segregation, since most specimens might not have been breeding where they were sampled (Furness 1987; Ryan et al. 2014). However this has been a useful proxy of breeding distribution as all incubating prions found at Golden Highway were *P. vittata*, which is consistent with carcasses in this site. Similarly birds found incubating in burrows and caves near the base and Admirals all conform to *P. vittata*, again substantiating the carcass data from these sites.

Topography and physical factors have been shown to influence nest site selection (Schramm 1986; Brandt et al. 1995; Ramos et al. 1997; Sullivan and Wilson 2001; Catry et al. 2003) and this study suggests that *P. vittata* on Gough Island may have a preference for steeper slopes with eastern aspect, as well as habitat broadly defined as fernbush given the general tendency of altitudinal segregation, and from west to east between the two species. While *P. macgillivrayi* may have a preference for more gentle slopes and open terrain with shorter vegetation, Sullivan and Wilson (2001) found that *P. vittata* selected areas with dense canopy cover and had a slight preference for steep slopes with an eastern aspect and softer soils at the Chatham Islands. However they found that *P. vittata* are more generalist in habitat selection compared to Chatam petrels, and fully utilised the available habitat at this breeding site. Steep slopes have been shown to support higher densities of burrowing petrels (e.g. Schramm 1986; Brandt et al. 1995; Catry et al. 2003). Steep terrain may be preferable for burrowing petrels for a number of reasons such as efficient drainage, less risk of collapse, less intensive excavation/refurbishment and providing quicker take-off, leading to improved predator escape (Stokes and Boersma 1991; Brandt et al. 1995). Skuas are important prion predators on Gough Island, and possibly force a selective pressure for habitat selection. Easier take-off could also be attributed to short vegetation and *P. belcheri* breeding at New Island in the Falklands have been shown to have a preference for shorter vegetation (Catry et al. 2003). Nevertheless, the occurrence of these habitats on Gough Island varies with slope and altitude, and it is difficult to disentangle all these factors.

Initially it was thought that elevation was a factor segregating the two morphs (Ryan et al. 2014) with *P. vittata* dominating the lowlands, but *P. macgillivrayi* breeds in Prion Cave which is at low elevation, and the Gonydale path and Golden Highway sites (similar elevation) are clearly dominated by different species. Similarly, Green Hill has the lowest mean bill width on the island, whereas Low Hump ridge immediately to the north has a much higher proportion of birds conforming to *P. vittata*. The only apparent explanatory variable between similar sites supporting the different species is that sites with *P. macgillivrayi* appear to contain more caves. However, not all *P. macgillivrayi* are confined to caves, as birds found incubating in burrows in *P. macgillivrayi* dominant sites have the morphology and breeding phenology typical of the species. Observations around the Base also found that *P. vittata* occasionally breed in caves, as they do in the Tristan da Cunha archipelago (P.G. Ryan pers. comm.; see chapter 3).

Prion Cave is dominated by *P. macgillivrayi*, and although a few individuals measured in this cave conform to *P. vittata*, 95% conform to *P. macgillivrayi* (**Table 2.2**). The fact that only two pairs of *P. vittata* have been found incubating in this site in September 2017, confirms that *P. vittata* breed at low density in this site. It is worth noting that *P. macgillivrayi* starts breeding before *P. vittata* chicks fledge, so that for the most part they are limited in the capacity to share breeding sites, although *P. macgillivrayi* could occupy failed *P. vittata* nests. However, this temporal overlap doesn't explain the distribution of *P. vittata*, who breed first and could select anywhere to do so. Unless *P. vittata* avoid habitat preferred by *P. macgillivrayi* in order to reduce chance of displacement. Thus it appears that both species are seemingly capable of occupying similar nesting habitat but there are probably species-specific preferences.

The population ratio estimate based on relative species proportions given in this study is likely inflated, given that much depends on the relative density in the different areas dominated by each species. *Pachyptila macgillivrayi* is probably more clumped, with high concentrations in cave areas, and *P. vittata* more widespread, and perhaps averaging higher density on an island-wide scale. However, the population estimates produced from combing species ratio with estimated habitat area suggests that *P. macgillivrayi* has a substantial population (up to one million pairs) on Gough Island and that the most recent population estimate of 100 000 pairs of this endangered species (BirdLife International 2017), based on the proportions in skua middens (Ryan et al. 2014), may be an underestimate. This finding provides further evidence to support the importance of Gough Island as the stronghold for both species.

Further research is needed to clarify the breeding distributions of the two prion species on Gough Island, both in unsampled areas to complete the island-wide map of species dominance, and at a finer scale to resolve whether there are areas where both species co-occur. Additional detailed categorizing of habitat types should be done in order to shed light on the actual drivers of spatial segregation. Such research, coupled with estimates of breeding densities, is crucial to make an up-to-date population estimate of both prion species breeding on Gough Island.

Chapter 3

Spatial distribution, activity patterns, trophic niche and habitat preference of *Pachyptila vittata* and *P. macgillivrayi*

ABSTRACT

This is the first study to examine the at-sea movements, activity patterns and oceanic habitat preference of prions from Tristan da Cunha and Gough Island. Using GLS and stable isotope data, I compared the spatial distribution and foraging behaviour of Broad-billed *Pachyptila vittata* and MacGillivray's Prions *P. macgillivrayi*. During their respective breeding seasons, *P. vittata* largely remained within 1500 km to the north-east of the colony whereas *P. macgillivrayi* occupied waters within 1000 km to the south of the colony. *Pachyptila vittata* departed and returned to the colony much earlier than *P. macgillivrayi*, and all tracked individuals except one *P. vittata* engaged in a pre-laying exodus. The *P. vittata* population from Tristan da Cunha departed and returned significantly later than their counterparts from Gough Island, providing evidence for temporal character displacement in sympatry with *P. macgillivrayi*. After breeding, both species showed a well-defined outward migration, with all moving west until the start of moult, except one *P. vittata* that moved east. Flight feather moult was identified by a marked reduction in the time spent in flight by both species post-breeding, which lasted 11 to 19 weeks, with *P. macgillivrayi* taking significantly longer. Moulting birds of both species targeted specific areas with little overlap within the Argentine Basin. Both species briefly returned to their colonies after moult was complete. During the remainder of the non-breeding period, both species were distributed more widely over the South Atlantic Ocean. Inter-specific spatial segregation was observed for most of the tracking period, especially in core areas with some overlap in peripheral distribution. *Pachyptila macgillivrayi* spent more time in flight, during both day and night, than *P. vittata*. Stable isotope ratios measured in flight feathers suggested that tracked individuals were typical of each species. δ^{15}N values suggest that *P. macgillivrayi* occupies a higher trophic level than *P. vittata*, which is consistent with its less specialized bill morphology. Habitat analysis revealed species-specific preferences for distance from the breeding colony, chlorophyll *a*, sea surface temperature and distance to seamount, but not for water depth. This study contributes to the growing number of studies tracking small petrels and sheds light on the ecological

segregation of these highly abundant species and improves the understanding of moult in prions.

INTRODUCTION

Spatial segregation is thought to be a key factor that eases competition in seabirds (Furness and Birkhead 1984; Chesson 2000; Lewis et al. 2001). However, this is not necessarily applicable where two species are extremely similar in morphology with a paucity of breeding locations (see Chapter 1). In such cases, the timing of activities such as breeding and moulting may be the main driver of ecological segregation (Friesen et al. 2007; Cherel et al. 2016; Whitehead et al. 2016; Taylor and Friesen 2017).

In birds, breeding, migration, and moult all increase energy demands and energy budgets govern the timing of these activities. For example, when not restricted by breeding several seabird species migrate, targeting more productive foraging zones in order to moult and build up body condition for the next breeding attempt (Phillips et al. 2007; Cherel et al. 2016; Grecian et al. 2016). The importance of the non-breeding period is well documented as well as how various factors during this time affect the population dynamics of seabirds in terms of breeding success and survival (Grosbois and Thompson 2005; Schroeder et al. 2009). However, specific aspects during this period, such as migration, core foraging areas and moult are not well understood in many seabird species.

The prions (*Pachyptila* spp.), are very similar in morphology, foraging techniques and diet, as such they are interesting species to study in terms of niche partitioning and community assembly rules (Cherel et al. 2002). Their distributions at sea have been poorly known because of their huge ranges, difficulty in identification at sea and few ring recoveries (Onley and Scofield 2007). Given technological advances that have reduced the size, mass and cost of loggers, there have been increasing numbers of studies examining at-sea spatial distribution and activity of smaller procellariiformes including prions (Rayner et al. 2008; Catry et al. 2009; Shaffer et al. 2009; Navarro et al. 2013; 2015; Quillfeldt et al. 2013; 2015a; 2015b; Cherel et al. 2016; Grecian et al. 2016).

Geolocation and feather stable isotope data imply that prions in the southwest Atlantic have species-specific patterns of migration and foraging, resulting in spatial segregation (Cherel et al. 2006; Quillfeldt et al. 2008; Quillfeldt et al. 2013; Cherel et al. 2014). Sympatrically breeding prions that are similar in size and feeding methods at the Kerguelen archipelago (Cherel et al. 2002) have been shown to exhibit spatial segregation at large scales during their non-breeding period (Quillfeldt et al. 2015b; Cherel et al. 2016). However, the two prion species that breed sympatrically on Gough Island – Broad-billed *Pachyptila vittata* and MacGillivray's Prions *P. macgillivrayi,* are closer in morphology compared to other prion species looked at in previous geolocation studies, making this a unique example.

I deployed geolocators on both prion species that breed sympatrically on Gough Island in order to investigate their movements, activity patterns, habitat preferences and isotopic niche. *Pachyptila macgillivrayi* has only recently been differentiated from *P. vittata* on Gough Island (Birdlife International 2017; P. Ryan unpublished data), attesting to their extremely similar appearance. Geolocators with an immersion sensor were used in combination with carbon and nitrogen stable isotope analysis of flight feathers, which broadly represent the latitude and trophic level at the time of moult (Hobson and Clark 1992; 1993; Bearhop et al. 2002). This method has been validated in the southern Indian Ocean (encompassing petrel feeding areas), with δ^{13}C signatures giving an indication of latitude (Jaeger et al. 2010) and δ^{15}N indicating trophic level (Cherel et al. 2010). In this way, the location of the moulting zones within broad oceanographic sectors can be inferred from the marked increase in the amount of time moulting birds spend sitting on the water. Given the difference in the timing of breeding between the two species, it is expected that there will be limited spatio-temporal overlap in distribution, activity patterns and habitat preference. It is also expected that these spatial distribution and activity patterns are also specific to and different within discrete periods of the yearly cycle (breeding, moulting, and nonbreeding) owing to the different time-energy budget, resources available and central-place restriction. The findings are important within the framework of understanding niche partitioning and ecological segregation between abundant, closely related seabirds.

METHODS

Fieldwork

Fieldwork for this chapter was carried out at the main island of Tristan da Cunha (37.07°S; 12.32°W) and Nightingale Island (approx. 20 km southwest the main island), where only *P. vittata* breeds, and Gough Island (40.32°S; 9.94°W), where *P. vittata* and *P. macgillivrayi* breed sympatrically. Some tracking devices were deployed at the main island, and for isotopic analysis of feathers a sample of fresh *P. vittata* carcasses was collected at Nightingale Island. Breeding is highly synchronous within prion species (Bretagnolle et al. 1990) and occurs roughly three months apart between species, with *P. vittata* laying in August-September and fledging by early December; while *P. macgillivrayi* lay from late November to early December and fledge in February-March (Ryan et al. 2014). Both species return to their nest sites during a post-breeding visit around February-March for *P. vittata* and July-August for *P. macgillivrayi.* Available information on moult pattern and phenology of prions is generally scarce (Marchant and Higgins 1990). In small petrels such as prions primary feathers are replaced following a simple pattern in order from the innermost (P1) first to the outermost (P10) last (Bridge 2006), with 3-4 inner primaries being replaced at the same time (PG Ryan unpublished data). Observations of adults in new plumage at the colony indicate that both species in this study replace all primary, secondary and tail feathers during the initial post-breeding exodus (Ryan 2007; C. Jones pers. obs).

To investigate the year-round spatial movements and activity patterns of the two species of prion, I attached leg-mounted miniaturized saltwater immersion geolocators (model C65, Migrate Technology Ltd.) that weighed approximately 1 g (< 1% of the average body mass for both species, ~150-230 g) and were fixed to plastic leg bands. Tagged individuals were marked with numbered steel rings on the other leg. Loggers were deployed at Gough Island on 18 *P. vittata* breeding in burrows near the 'Golden Highway' (250 m above sea level, see Chapter 2) and in a small cave in the sea cliffs near the meteorological station from 19-21 September 2014. Fifteen *P. macgillivrayi* breeding in 'Prion Cave' were tagged during incubation from 25 November – 03 December 2014. At Tristan, loggers were deployed on 15 *P. vittata* attending chicks in a cave accessible only from the sea under the Hillpiece on 04 November 2014. The birds were captured by hand, and their nests marked. Breeding sites were revisited and devices retrieved in the following breeding season.

Stable isotopes

Primary feathers were collected from the birds equipped with GLS at recapture in 2015. Also in September-October 2013, feather samples were collected from 24 birds of each species found dead on Gough Island and from 20 *P. vittata* from Nightingale Island. The dead birds were fully grown (not fledglings), killed by Brown Skuas *Stercorarius antarcticus* before or during the breeding season. In each case approximately 10 mm was cut from the tip of primary feather P1 (GLS birds) or P2 (dead birds), and similar-sized sections of the basal part of the inner vane of primaries P5 and P9 were collected in order to gather sequential isotopic information over the period of primary moult. The difference in feathers samples between GLS and dead birds was due to collection by different people. The isotopic signatures of P1 and P2 are likely to be very similar because prions replace the inner primaries synchronously. In addition, the feathers compared between GLS and dead birds were grown in different years. During retrieval of geolocators, one individual from Tristan da Cunha only had P1 collected, reducing the sample size from GLS tracked birds. Feather samples were placed individually in plastic bags and stored frozen until processing in the laboratory. Isotopic measurements were made on the three sampled primary feathers per individual to assess species and population isotopic niches during moult.

In order to investigate the relationship between trophic level and foraging strategy in relation to bill morphology, numbers of palatal lamellae were determined with the aid of a dissecting microscope from a sample of carcasses of *P. vittata*, *P. macgillivrayi* and *P. salvini* from Gough and Marion Island, respectively. Bill width and culmen length of these carcasses were also measured using Vernier callipers to the nearest 0.1 mm.

Feather sample preparation and isotopic analysis were performed at the Stable Light Isotope Unit, University of Cape Town, South Africa. Each feather sample was cleaned of surface lipids and contaminants using 2:1 chloroform:methanol solution for two minutes followed by two successive methanol rinses and then by two distilled water rinses (a few seconds each rinse). Feather samples were then oven dried at 40°C for 48 hours and homogenized by cutting them into small fragments. Sub-samples (~0.4 mg) were weighed in tin cups with a micro balance (Sartorius M2P) accurate to the nearest microgram. Carbon and nitrogen isotope ratios were determined, using established methods, by combusting samples in a Flash 2000 organic elemental analyzer and passing gasses through a Delta V Plus isotope ratio mass spectrometer via a Conflo IV gas control unit (Thermo Scientific). Conventional notation was used when expressing isotopic signatures ($\delta X = [R_{sample}/R_{standard}) - 1] \times 1000$) where X is ^{13}C or ^{15}N, R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ and $R_{standard}$ is Vienna Pee-Dee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measures of internal laboratory standards were used to correct for any instrument error. Indicated measurement errors (±1 SD) of standards are given as follows: Merck gel - $\delta^{13}C = 0.17‰$, $\delta^{15}N = 0.07‰$, valine - $\delta^{13}C = 0.18‰$, $\delta^{15}N = 0.11‰$ and seal bone - $\delta^{13}C = 0.19‰$, $\delta^{15}N =$

0.06‰. Internal laboratory standards used for replicate measurement were calibrated against International Atomic Energy Agency standards.

Data processing and analysis

Tracking data covered the period September 2014 to August 2015 for *P. vittata* and December 2014 to November 2015 for *P. macgillivrayi* (i.e. one yearly cycle per species). Geolocators provide two position estimates per day based on light levels, positions have an associated error of approximately 186 ± 114 km (Phillips et al. 2004). Light data were processed using Intiproc v1.03 software (Migrate Technology Ltd.) by checking for the integrity of light curves and to fit dawn and dusk times, as well as to estimate the latitude from day length and longitude from the time of local mid-day relative to Greenwich Mean Time. A sun elevation angle of -6° was assumed, based on known positions obtained during calibration of the loggers carried out at the colony before and after each deployment. All estimated locations were examined in QGIS v2.14 (Free Software Foundation, Inc., Boston, MA) and any erroneous positions, either associated with interference to light curves at dawn or dusk, or within 14 days of the equinoxes when latitudes are unreliable, were excluded from further analyses. The unfiltered data were used to obtain information about longitudinal movements during the equinoxes, e.g. to define the timing of return migration that partly overlapped with the equinoxes. After processing, 7011 and 4128 locations were retained for *P. vittata* and *P. macgillivrayi*, respectively (approximately 80% of the original location estimates).

The immersion sensor on the loggers tested for saltwater immersion every 6 seconds. The number of positive tests was recorded for each 5-minute period, providing a value that ranged from 0 (continuously dry) to 50 (continuously wet). Each 5-minute period was categorised as daylight or darkness using sunset and sunrise times estimated from the thresholds in light curves recorded by the logger. Using established methods for activity analysis (Phillips et al. 2007b; Catry et al. 2009; Grecian et al. 2016), the activity data were integrated with a custom script using R v. 3.1.0 (R Core Team 2016) that summarised the data into the daily proportion of time spent flying during daylight and darkness (each consecutive light and dark period), as well as the total time spent per day in flight and on the water. The duration and number of flight bouts per day were also calculated, where flight bouts were defined as any continuous sequence of 5-minute periods of completely dry (0) values. This method is likely to underestimate the number of flight bouts, as birds may engage in several short flights within

5 minutes. However, Phalan et al. (2007) found a close correlation between bouts derived from lower and higher resolution loggers, indicating that bouts are adequate as proxies of activity.

Birds were not sexed for this study; prions are sexually monomorphic and feeding behaviour has not been found to vary between males and females in other species (Quillfeldt et al. 2013; Cherel et al. 2016). Data from breeding, non-breeding and pre-lay exodus periods were analysed (**Table 3.2**). The start of the non-breeding period was determined by departure from the colony, defined as the date that an individual moved >500 km from the colony with a clear pattern of outward movement (Grecian et al. 2016). The end of the non-breeding period was determined by scrutinizing light and activity data which indicated the date that an individual first spent a day in a nesting burrow upon returning to the breeding colony. The pre-laying exodus was defined as the time between the last day in a burrow during the pre-breeding occupation of burrows and the first day in a burrow prior to laying. The non-breeding period was divided into moulting and non-moulting periods based on data from the immersion sensor. Prions have reduced flight ability during moult (Cherel et al. 2016), so the moulting period for each individual was defined by a protracted period of reduced time spent in flight. The percentage of time spent in flight each day was examined to assign start and end dates to the moult period. This window was readily identified by a marked decrease in flight activity at the onset of moult, followed by a sharp increase when moult presumably was more or less complete (see Cherel et al. 2016). At-sea activity characteristics were compared between species and between daylight and darkness (**Table 3.4**).

Foraging distribution was inferred using kernel analysis of filtered locations (Phillips et al. 2004). Individual spatial use throughout the whole tracking period was investigated by producing 90% (general use) and 50% (core) utilization distributions (UDs) for each individual, using kernel analysis with a fixed smoothing parameter of 200 km (Phillips et al. 2006). Individual location estimates were grouped by species and split into respective periods (breeding, moulting, non-moulting, pre-lay exodus, etc.) in order to create stage-specific core and general use areas for each species. Kernel analyses were performed in a Lambert equal-area azimuthal projection centred on the South Pole using QGIS v2.14 and the Heatmap plugin. Spatial overlap of *P. vittata* (BBP) and *P. macgillivrayi* (MP) was determined by overlaying UDs and calculating the area of overlap (A_O, km^2) using the intersect tool in QGIS. The percentage of area shared by both species (**Table 3.3**) was estimated as:

$$\%Area\ Overlap = \frac{A_O}{[(A_{BBP} - A_O) + (A_{MP} - A_O) + A_O]} \times 100$$

after Tranquilla et al. (2013) and Hedd et al. (2014).

Environmental data

Habitat analysis was approached following the methods described by Grecian et al. (2016). To characterise the marine environment I extracted bathymetry data at one minute resolution from the ETOPO1 database (Amante and Eakins 2009) and global monthly chlorophyll *a* and sea surface temperature (SST, 11 µ night-time) composite data at 4 km^2 resolution from the MODIS instrument on board the Aqua (EOS PM) satellite (http://oceancolor.gsfc.nasa.gov/). I included distance to seamounts following Grecian et al. (2016) using the Global Seamount Database (Wessel 2001), and as preference is a function of availability I calculated distance to breeding colony. All data were projected to a custom Lambert Azimuthal Equal Area projection centred on 45°S and 20°W.

I took a use-availability approach to examine habitat use during the non-breeding period, and combined the geolocation presence points with pseudo-absences generated randomly from across the species range at a 5:1 absence to presence ratio. To incorporate the error associated with geolocation in our estimate of habitat preference, I generated 50 random points around each presence or pseudo-absence from a bivariate Gaussian distribution with mean and standard deviation that approximated that associated with geolocation (Phillips et al. 2004). I then extracted the mean of the environmental variable sampled by each set (Grecian et al. 2016).

I assessed habitat preference by exploring the relationship between prion occurrence based on GLS data and these environmental covariates using binomial generalized additive mixed models (GAMMSs) fitted with the package mgcv (Wood 2006) in R v. 3.1.0 (R Core Team 2016). Model estimates were assessed on the exponential scale due to the use of pseudo-absences (Boyce 2006). I included distance to colony, depth, SST, chlorophyll *a* and distance to seamount as covariates in the global model with cubic regression splines fitted with a maximum of 5 knots; superfluous knots were penalized during model fitting. I $\log_{10}$

transformed CHL prior to use and included an individual-level random effect as a spline term. Each covariate was first fitted with species as a factor interaction, and then compared against a model without the species interaction. Model selection was based on Akaike's Information Criterion (AIC), with the species interaction dropped if its inclusion did not improve the model by more than 2 ΔAIC relative to the lowest AIC. Variance inflation factors revealed no multicollinearity between covariates (VIFs < 3) and variograms of model residuals did not revealed any spatial autocorrelation in final models.

Statistical analyses

Univariate statistical comparisons of phenology, spatial data, flight patterns and isotope data were all normally distributed and parametric tests were used. Univariate statistical tests were conducted using XLSTAT v2014.5.03 (Addinsoft SARL, Paris). Data are shown as means±1 standard deviation (SD) unless otherwise indicated.

RESULTS

Thirteen devices (39%) were recovered from *P. vittata* (9 from Gough (50%) and 4 from Tristan (27%)), and 8 devices (53%) from *P. macgillivrayi*. Differences in recovery rates (**Table 3.1**) were mainly due to logistical constraints limiting the number of visits to deployment sites; the sea cave at Tristan da Cunha was only visited once in the year after deployment. Previous studies indicate that geolocators do not affect the behaviour of prions (Quillfeldt et al. 2013; Quillfeldt et al. 2015; Cherel et al. 2016) and this study had similar findings: although difficult to assess due to severe mouse predation, breeding performance of deployment nests appeared unaffected when comparing deployment nests to a control group of monitored nests (**Table S3.2**) and the comparison of δ^{13}C and δ^{15}N values of feathers from tracked individuals and control birds (killed by skuas) indicated that their foraging ecology was unchanged.

Table 3.1. Sample sizes of prions with geolocators (GLS) at deployment/recovery, and for primary feather stable isotope analysis from deployment birds.

	GLS		Tracks		Feathers
	Deployed	Retrieved	All	Complete	collected
Species	n	n (%)	n	n	n
P. vittata (Tristan)	12	4 (33)	4	4	4
P. vittata (Gough)	18	9 (50)	9	9	9
P. macgillivrayi	15	8 (53)	8	3*	8

*5 birds were recaptured on their return to the island in September, thus missing the pre-laying period.

Phenology

The annual cycle of the GLS birds was in accordance with the known phenology of the two species at their colonies (**Table 3.2**). Post-breeding departure dates of adult *P. vittata* occurred from late October to November and arrival occurred in July. Birds from Tristan departed and returned on average 15 and 17 days later, respectively, compared to their Gough Island counterparts. *Pachyptila macgillivrayi* left the colony in late January to early February, on average 91 days later than *P. vittata* from Gough Island. The transient reoccupation of the burrows of both species was verified, with light data indicating that 12 of 13 *P. vittata* spent 1–7 days in burrows at the colony from 2 February to 18 March at Gough Island and 27 February to 10 April at Tristan da Cunha; one *P. vittata* from Gough Island apparently did not spend a day in a burrow but did return to the vicinity of the island during this time, possibly only coming ashore at night. All eight *P. macgillivrayi* spent 1–7 days in burrows from 30 June to 16 September during their post-moult reoccupation. The length of the non-breeding period did not differ significantly between species or populations (**Table 3.2**). After returning to their respective colonies, all three *P. macgillivrayi* that were tracked for a whole year and 12 of 13 (92%) *P. vittata* that returned to breed in 2015 respectively, engaged in a pre-laying exodus. *Pachyptila vittata* from Tristan returned to the colony and started their pre-lay trip significantly later than their Gough Island counterparts; however the onset of breeding did not differ because Tristan birds had shorter pre-laying trips (**Table 3.2**). The length of the pre-laying exodus did not differ significantly between *P. macgillivrayi* and *P. vittata* from Tristan, although this may be an artefact of the small sample size for *P. macgillivrayi*.

Table 3.2. Summary of the main features of the various phases throughout the tracking period of *P. vittata* (BBP) and *P. macgillivrayi* (MP) from Gough and Tristan da Cunha in 2014-15. Values are means ± SD. Values not sharing the same superscript letter are significantly different at the 0.05 level (ANOVA, posthoc Tukey's HSD multiple comparison tests).

	BBP Gough	**BBP Tristan**	**MP Gough**	**ANOVA results**
Non-breeding Period	**(n=9)**	**(n=4)**	**(n=8)**	
Departure date	29/10/2014 (±11)^{a}	13/11/2014 (±10)^{b}	28/01/2015 (±7)^{c}	$F_{(2, 18)}$=203.1, p<0.0001
Pre-breeding arrival date	10/07/2015 (±7)^{a}	27/07/2015 (±17)^{b}	12/10/2015 (±8)^{c}	$F_{(2, 18)}$=211.0, p<0.0001
Duration (days)	254 (±15)	256 (±23)	257 (±15)	$F_{(2, 18)}$=0.08, p=0.924
Total distance (km)	36872 (±3238)	37833 (±6411)	41679 (±8930)	$F_{(2, 18)}$=1.1, p=0.352
Max distance from colony	2957 (±396)^{a}	3126 (±254)^{ab}	3468 (±87)^{b}	$F_{(2, 18)}$=6.7, p=0.007
Travel speed (km/day)	145 (±13)	147 (±12)	161 (±25)	$F_{(2, 18)}$=1.8, p=0.199
Moulting Period	**(n=9)**	**(n=4)**	**(n=8)**	
Start date	09/11/2014 (±4)^{a}	27/11/2014 (±10)^{b}	04/02/2015 (±7)^{c}	$F_{(2, 18)}$=400.7, p<0.0001
End date	12/02/2015 (±11)^{a}	03/03/2015 (±4)^{b}	30/05/2015 (±13)^{c}	$F_{(2, 18)}$=212.5, p<0.0001
Duration (days)	95 (±8)^{a}	96 (±8)^{a}	115 (±10)^{b}	$F_{(2, 18)}$=11.4, p=0.001
Latitude Centroid (S°)	39.4 (±0.8)^{a}	40.3 (±0.3)^{a}	44.6 (±0.8)^{b}	$F_{(2, 18)}$=108.9, p<0.0001
Longitude Centroid (W°)	25.4 (±19.8)^{a}	36.5 (±5.4)^{ab}	43.2 (±2.5)^{b}	$F_{(2, 18)}$=3.8, p=0.043
Post Moult Transient Return	**(n=9)**	**(n=4)**	**(n=8)**	
Post moult return date	22/02/2015 (±15)^{a}	10/03/2015 (±11)^{a}	23/07/2015 (±16)^{b}	$F_{(2, 18)}$=250.3, p<0.0001
Post moult departure date	11/03/2015 (±14)^{a}	30/03/2015 (±15)^{a}	31/08/2015 (±14)^{b}	$F_{(2, 18)}$=352.3, p<0.0001
Total duration (days)	17 (±19)	20 (±18)	40 (±24)	$F_{(2, 18)}$=2.7, p=0.094
Duration in burrow (days)	3 (±3)	3 (±2)	5 (±2)	$F_{(2, 18)}$=1.4, p=0.268
Pre-Laying Exodus	**(n=8)**	**(n=4)**	**(n=3)**	
Pre-layarrival date	10/07/2015 (±7)^{a}	27/07/2015 (±17)^{b}	12/10/2015 (±8)^{c}	$F_{(2, 18)}$=211.0, p<0.0001
Pre-lay departure date	28/07/2015 (±9)^{a}	21/08/2015 (±7)^{b}	04/11/2015 (±2)^{c}	$F_{(2, 12)}$=190.7, p<0.0001
Pre-lay return duration (days)	17 (±11)	25 (±13)	21 (±14)	$F_{(2, 13)}$=0.5, p=0.597
Pre-lay duration in burrow	4 (±3)	6 (±2)	6 (±5)	$F_{(2, 13)}$=1.1, p=0.350
Pre-lay exodus duration (days)	30 (±16)^{a}	18 (±4)^{ab}	21 (±6)^{b}	$F_{(2, 13)}$=4.6, p=0.032
Breeding arrival date	01/09/2015 (±9)^{a}	08/09/2015 (±7)^{a}	26/11/2015 (±3)^{b}	$F_{(2, 13)}$=128.9, p<0.0001

Spatial distribution

Near complete spatial segregation was observed between the two species for most of the year (**Figure 3.2**). At the 50% UD, overlap was observed in only three months (May, August and October) but there was some marginal overlap at the 90% UD in most months with only March showing complete segregation. The month of highest overlap was May, when there was 29% overlap at the 90% UD and 22% at the 50% UD. This corresponds to when *P. macgillivrayi* are moulting and *P. vittata* have departed the breeding colony after their post-moult transient return. Other months of relatively high overlap (August and October) occurred when both species are near their breeding colony during pre-breeding or breeding phases (**Table 3.3**).

Breeding period

Pachyptila vittata and *P. macgillivrayi* mostly remained within 1500 km and 1000 km of their colonies during their respective breeding seasons; their ranges were more constrained compared the non-breeding period (see below). Breeding *P. vittata* mostly remained in the vicinity of Gough Island and Tristan da Cunha or foraged north-east toward South Africa in sub-tropical waters, while *P. macgillivrayi* mostly foraged south-east to sub-Antarctic waters. There was little spatial overlap (<5%) at the 50% UD and overlap observed at the 90% UD was around their breeding colonies (**Figure 3.1**).

Non-breeding period

Similar movement patterns were observed when birds left their colonies after breeding. Both species showing a well-defined outward migration (defined as the time between departure from the colony to the start of moult), lasting on average 11±9 and 7±7 days for *P. vittata* and *P. macgillivrayi* respectively. All individuals of both species migrated in a westerly direction, except one *P. vittata* which migrated southeast. Spatial overlap was mainly evident at the 90%UD, overall showing significant spatial segregation during this period at sea. Latitudinal segregation was minimal (**Figure 3.1**), although *P. macgillivrayi* moved marginally farther south than *P. vittata*. Longitudinal difference was more apparent, with *P. macgillivrayi* moving farther west than *P. vittata* (**Figure 3.1**). Neither species displayed well-defined inward migration to their breeding ground in late winter; gradually returning to the vicinity of the breeding islands over a period of several weeks.

Timing and location of moult

Throughout the tracking period *P. vittata* and *P. macgillivrayi* spent an average of 43.2±5.5% and 46.1±5.1% of their time in flight per day respectively. However, relatively soon after breeding, activity patterns of both species showed a sharp decline in the proportion of each day spent in flight, presumably coinciding with the onset of primary moult (**Figure 3.2**). During moult the daily flight proportion of *P. vittata* and *P. macgillivrayi* averaged 19.7±3.0% and 23.5±4.7%, respectively.

Duration of moult in *P. vittata* was the same for birds from Gough Island (95±8 days) and Tristan (96±8 days), but Gough birds started to moult significantly earlier (9 November ±4 days) than their Tristan counterparts (27 November ±10 days; **Table 3.2**). *Pachyptila macgillivrayi* started to moult significantly later (4 February ±7 days) than *P. vittata* and took approximately 20 days longer (115±10 days, **Table 3.2**). *Pachyptila vittata* began their transient reoccupation of burrows an average of 8±8 days after moult ended. *Pachyptila macgillivrayi* spent substantially more time at sea after completing moult (53±12 days) compared to *P. vittata*.

Pachyptila vittata moulted mostly in subtropical waters, whereas *P. macgillivrayi* moulted further south and west in sub-Antarctic waters (**Figure 3.1**, **Table 3.2**). Spatial segregation was more pronounced during moult than the remainder of the non-breeding period, with marginal spatial overlap between species, 2.7% at the 50% UD and 11.2% at the 90% UD.

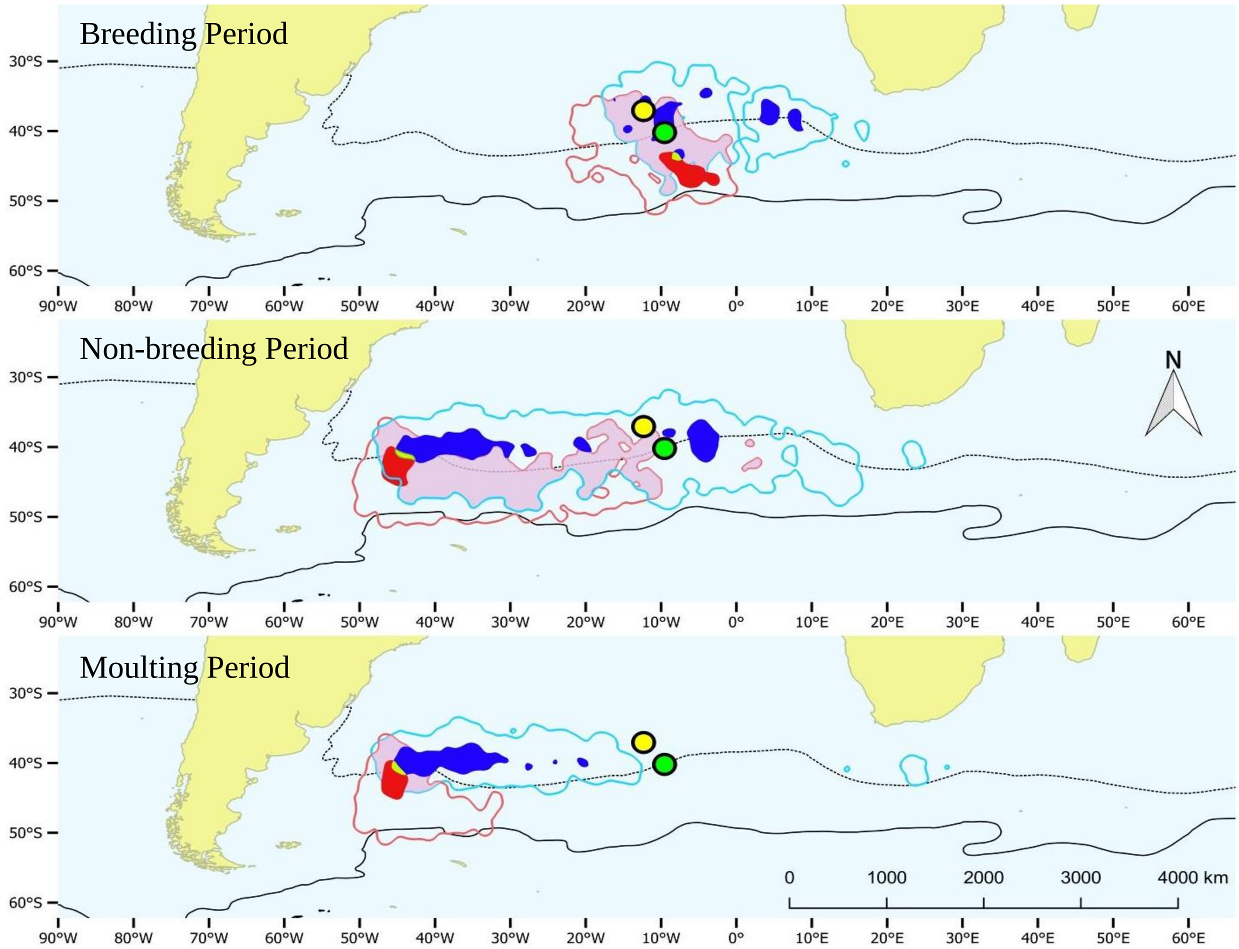

Figure 3.1. Density contours resulting from kernel estimation of geolocation patterns of *P. vittata* (blue) and *P. macgillivrayi* (red) prions at breeding, non-breeding and moult periods. Darker tones show the 50% core utilization density, while contours show the 90% general use utilization density. Purple and green shades are the species overlap at the 90% and 50% UD respectively. Yellow circle is Tristan da Cunha and green circle is Gough Island. Antarctic Polar Front (solid line) and Sub-Tropical Front (dashed line) are shown.

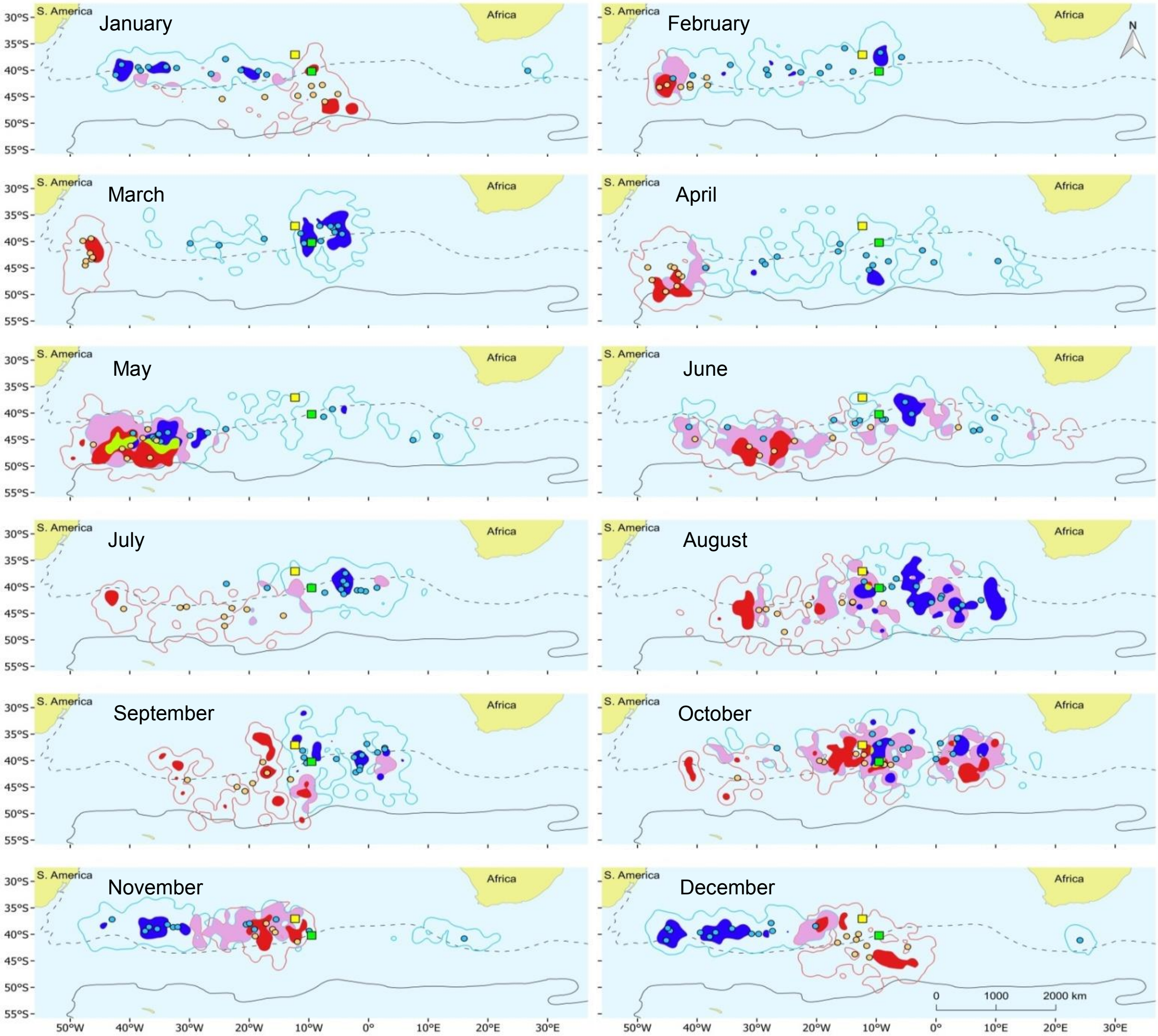

Figure 3.2. Density contours resulting from kernel estimation of geolocation patterns of *P. vittata* (blue) and *P. macgillivrayi* (red) prions at monthly intervals. Darker tones show the 50% core utilization density, while contours show the 90% general use utilization density. Purple and green shades are the species overlap at the 90% and 50% UD, respectively. Small dots represent mean monthly coordinates for each individual - *P. vittata* (blue) and *P. macgillivrayi* (orange). Yellow square is Tristan da Cunha and green square is Gough Island. Antarctic Polar Front (solid line) and Sub-Tropical Front (dashed line) are shown.

Table 3.3. Summary of spatial overlap by month.

Month	90% UD Overlap (%)	50% UD Overlap (%)
January	3	0
February	9	0
March	0	0
April	4	0
May	29	22
June	26	0
July	4	0
August	19	1
September	6	0
October	36	4
November	23	0
December	6	0

Activity patterns

Both species spent time in flight both during the day and at night. There were no significant inter-population differences in activity patterns between *P. vittata* from Gough Island and Tristan da Cunha (**Table 3.4**). During the breeding period, *P. macgillivrayi* spent a greater proportion of time in flight overall (**Table 3.4**) and significantly more time flying (13.5±1.0 h) than sitting on the water (10.5±1.0 h; t-test t_{14}=6.4, p<0.0001), whereas *P. vittata* spent equal time flying (11.9±1.5 h) and on the water (12.1±1.5 h; t-test, t_{22}= -0.6, p=0.524), but this was not reflected in daily flight bouts or average bout duration, where there was no significant difference between the two species (**Table 3.3**). Both species spent proportionately equal time in flight during day and night (t-test, BBP: t_{22}= -1.9, p=0.069; MP: t_{14}= -2.0, p=0.075).

During the non-breeding period, there were few inter-specific differences in time on the water, with only flight time during the day and number of flight bouts significantly higher in *P. macgillivrayi* than *P. vittata* (**Table 3.3**). This pattern was broadly mirrored in the moult period, which occupied ~35% of the non-breeding period (**Tables 3.2 and 3.3**). The decrease in flight time during moult was observed during day and at night, but unlike the breeding and non-moulting periods, both species appeared to spend proportionately more time on the water at night (**Table 3.3**). After moulting there were greater differences between the species. During this time *P. macgillivrayi* spent more time in flight (overall and by day and night) mainly due to a greater number of flight bouts, since flight bout duration was not significantly different. Proportions of flight activity were also broadly similar to breeding prions (**Table 3.4**).

During the pre-laying exodus, *P. vittata* activity patterns did not differ significantly from the non-moulting and breeding periods (ANOVA, $F_{4,\,58}$=65.9, p=0.194). There were too few data for *P. macgillivrayi* (n=3) to make a meaningful comparison between the two species. Nonetheless the two species do not differ significantly across all activity parameters analysed during this period (**Table 3.3**). The few *P. macgillivrayi* sampled spent significantly less time in flight compared to breeding and non-moulting periods (ANOVA, $F_{4,\,30}$=73.9, p<0.0001).

Table 3.4. At-sea activities during various periods of *P. vittata* (BBP) and *P. macgillivrayi* (MP) tracked from Tristan da Cunha and Gough Islands in 2014-15. Values are means±1 SD. Values not sharing the same superscript letter are significantly different at the 0.05 level.

	Gough BBP	**Tristan BBP**	**All BBP**	**MP**	**ANOVA results**
Breeding Period	**(n=9)**	**(n=3)**	**(n=12)**	**(n=8)**	
Fight time (%)	51.3 (±4.3)^{ab}	43.0 (±7.4)^{a}	49.2 (±6.1)^{a}	56.4 (±4.0)^{b}	$F_{(3, 28)}$=5.5, p=0.004
Flight time (h/d)	12.4 (±1.0)^{ab}	10.3 (±1.8)^{a}	11.9 (±1.5)^{a}	13.5 (±1.0)^{b}	$F_{(3, 28)}$=5.3, p=0.005
Flight time during daylight (%)	48.3 (±4.9)^{ab}	42.5 (±7.0)^{a}	46.9 (±5.8)^{a}	54.3 (±3.6)^{b}	$F_{(3, 28)}$=5.1, p=0.006
Flight time at night (%)	54.6 (±4.9)^{ab}	44.0 (±7.7)^{a}	52.0 (±7.2)^{a}	60.7 (±8.3)^{b}	$F_{(3, 28)}$=4.9, p=0.007
Daily flight bouts (n)	7.7 (±1.6)	6.0 (±2.6)	7.3 (±1.9)	8.2 (±0.8)	$F_{(3, 28)}$=1.2, p=0.312
Flight bout duration (min)	63.4 (±8.5)	54.8 (±7.5)	61.3 (±8.8)	53.8 (±5.2)	$F_{(3, 28)}$=2.7, p=0.064
Non-Breeding Period	**(n=9)**	**(n=4)**	**(n=13)**	**(n=8)**	
Fight time (%)	35.6 (±3.7)	34.1 (±4.9)	35.1 (±4.0)	39.4 (±3.1)	$F_{(3, 30)}$=2.6, p=0.070
Flight time (h/d)	8.5 (±0.9)	8.2 (±1.2)	8.4 (±1.0)	9.4 (±0.7)	$F_{(3, 30)}$=2.6, p=0.070
Flight time during daylight (%)	33.9 (±3.9)^{a}	33.2 (±5.5)^{a}	33.7 (±4.2)^{a}	40.8 (±1.5)^{b}	$F_{(3, 30)}$=7.0, p=0.001
Flight time at night (%)	35.8(±4.4)	34.1 (±4.2)	35.3 (±4.2)	37.5 (±4.7)	$F_{(3, 30)}$=0.7, p=0.572
Daily flight bouts (n)	5.9 (±1.0)^{a}	6.0 (±0.7)^{ab}	5.9 (±0.9)^{a}	7.2 (±0.6)^{b}	$F_{(3, 30)}$=4.6, p=0.009
Flight bout duration (min)	55.4 (±6.4)	50.0 (±1.9)	53.7 (±5.9)	50.3 (±3.8)	$F_{(3, 30)}$=1.8, p=0.176
Moulting Period	**(n=9)**	**(n=4)**	**(n=13)**	**(n=8)**	
Fight time (%)	19.3 (±3.1)	20.6 (±2.8)	19.7 (±3.0)	23.5 (±4.7)	$F_{(3, 30)}$=2.6, p=0.069
Flight time (h/d)	4.6 (±0.8)	5.0 (±0.7)	4.7 (±0.7)	5.7 (±1.1)	$F_{(3, 30)}$=2.7, p=0.066
Flight time during daylight (%)	23.1 (±4.1)^{a}	23.1 (±3.4)^{a}	23.1 (±3.8)^{a}	30.2 (±4.7)^{b}	$F_{(3, 30)}$=6.1, p=0.002
Flight time at night (%)	12.2 (±3.3)	15.9 (±2.0)	13.3 (±3.4)	16.4 (±5.4)	$F_{(3, 30)}$=2.2, p=0.109
Daily flight bouts (n)	3.8 (±0.9)	4.4 (±0.6)	4.0 (±0.8)	4.7 (±1.1)	$F_{(3, 30)}$=2.1, p=0.119
Flight bout duration (min)	44.6 (±4.1)	40.1 (±1.2)	43.2 (±4.0)	45.1 (±5.4)	$F_{(3, 30)}$=1.4, p=0.254
Non-Moulting Period	**(n=9)**	**(n=4)**	**(n=13)**	**(n=8)**	
Fight time (%)	45.6 (±5.3)^{a}	42.5 (±5.6)^{a}	44.6 (±5.3)^{a}	52.9 (±2.9)^{b}	$F_{(3, 30)}$=6.3, p=0.002
Flight time (h/d)	10.9 (±1.3)^{a}	10.2 (±1.3)^{a}	10.7 (±1.3)^{a}	12.7 (±0.7$^{)b}$	$F_{(3, 30)}$=6.3, p=0.002
Flight time during daylight (%)	40.4 (±5.6)^{a}	39.6 (±6.5)^{a}	40.1 (±5.6)^{a}	49.9 (±2.1)^{b}	$F_{(3, 30)}$=7.3, p=0.001
Flight time at night (%)	50.4 (±5.3)^{ab}	45.2 (±4.9)^{a}	48.8 (±5.6)^{a}	55.7 (±5.4)^{b}	$F_{(3, 30)}$=4.2, p=0.013
Daily flight bouts (n)	7.3 (±1.7)^{a}	6.9 (±0.9)^{a}	7.2 (±1.5)^{a}	9.2 (±0.8)^{b}	$F_{(3, 30)}$=4.4, p=0.011
Flight bout duration (min)	59.0 (±7.9)	53.8 (±2.0)	57.4 (±7.0)	52.5 (±4.4)	$F_{(3, 30)}$=1.8, p=0.176
Pre-Lay Exodus	**(n=8)**	**(n=4)**	**(n=12)**	**(n=3)**	
Fight time (%)	45.5 (±5.1)	43.5 (±10.3)	44.8 (±6.8)	35.8 (±9.2)	$F_{(3, 23)}$=1.5, p=0.245
Flight time (h/d)	10.9 (±1.2)	10.4 (±2.5)	10.7 (±1.6)	8.6 (±2.2)	$F_{(3, 23)}$=1.5, p=0.246
Flight time during daylight (%)	41.2 (±5.4)	45.9 (±8.3)	42.8 (±6.5)	37.0 (±9.9)	$F_{(3, 23)}$=1.1, p=0.382
Flight time at night (%)	49.1 (±6.2)	41.0 (±13.7)	46.4 (±9.6)	34.0 (±8.7)	$F_{(3, 23)}$=2.2, p=0.111
Daily flight bouts (n)	7.1 (±1.3)	8.4 (±1.9)	7.6 (±1.5)	7.6 (±1.9)	$F_{(3, 23)}$=0.6, p=0.615
Flight bout duration (min)	56.4 (±7.3)	46.8 (±5.2)	53.2 (±8.0)	49.6 (±7.5)	$F_{(3, 23)}$=1.7, p=0.198

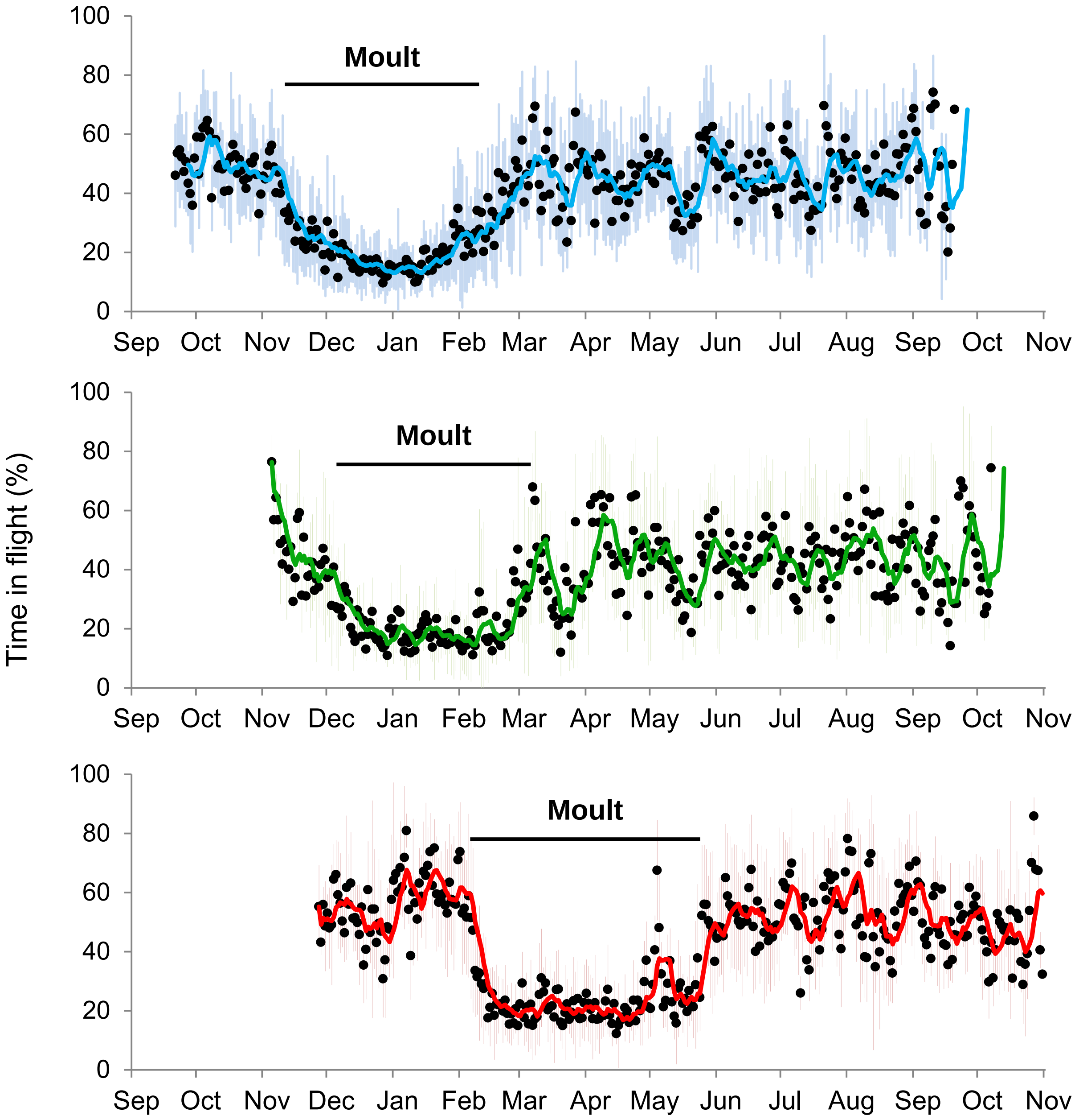

Figure 3.3. Time spent in flight (%) over the annual cycle based on immersion data from miniaturized saltwater immersion geolocators as a proxy of daily activity patterns of *P. vittata* from Gough (blue), Tristan (green) and *P. macgillivrayi* (red) tracked in 2014-15. Trend line is the 7-day running average. Values are daily means±SD.

Stable isotopes

Isotopic data were obtained on 262 primary feathers from 88 individuals, including 58 measurements from tracked birds and 204 measurements from control birds (**Table 3.5**). Comparison of 2013 and 2015 birds across comparable primaries revealed significant difference in δ^{13}C for P5 in both species (t-test, BBP: t_{17}= -2.6, p=0.037; MP: t_{14}=3.4, p<0.0001) and P1/P2 in *P. vittata* (t_{24}= -4.4, p<0.0001), with consistently lower values in GLS birds, suggesting apparent changes in latitudinal position across seasons, although this could also be attributable to shifts in oceanic δ^{13}C across seasons. No differences were observed in δ^{15}N values between GLS and dead birds for both species (all p>0.05), suggesting that all birds in the sample population fed at similar trophic levels across seasons. Inter-population variability was lower when comparing birds from Nightingale and Gough Island (**Table 3.4; Figure 3.4**). Primaries P1/2 and P5 of *P. macgillivrayi* were consistently more enriched with δ^{15}N than those of *P. vittata* (**Table 3.5; Figure 3.4**). Considering the respective timing of moult for each species (see **Table 3.2**), P1 from *P. macgillivrayi* and P9 from *P. vittata* are replaced at roughly the same time (February) and there is no significant difference between δ^{13}C and δ^{15}N in these feather samples for either GLS or other birds. This suggests that the two species occupy similar latitude and trophic level when *P. macgillivrayi* is starting moult and *P. vittata* is nearing the end of moult. This inference is consistent with the results obtained from the geolocators, although the two species were segregated longitudinally at this time (**Figure 3.2**). Both species replaced most primaries in subtropical waters, characterised by δ^{13}C values greater than -18.3‰. Only a few feathers had isotopic signals typical of more sub-Antarctic waters (-21.2 to -18.3‰) (Jaeger et al. 2010).

Bill width was related to the number of palatal lamellae, with the number of lamellae increasing with increasing bill width across species (**Figure S3.1**). Thus the mean number of lamellae was significantly higher in *P. vittata* than *P. macgillivrayi*, and lowest in *P. salvini* (**Table S3.1).**

Table 3.5. $\delta^{15}N$ and $\delta^{13}C$ values from primary feathers (P1/2, P5, P9) of *P. vittata* and *P. macgillivrayi*, grown during the non-breeding period, collected from GLS tracked birds from Tristan and Gough in 2015 and dead birds from Nightingale and Gough in 2013. Values are means ± SD.

		2015 (GLS)			2013 (dead)		
Species	Population	Feather	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Feather	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
P. vittata	Gough	P1 (n=9)	9.9 (±2.2)	-18.0 (±0.5)	P2 (n=24)	11.4 (±2.1)	-16.8 (±0.7)
		P5 (n=9)	12.1 (±1.6)	-17.0 (±0.8)	P5 (n=24)	12.2 (±1.7)	-16.5 (±0.6)
		P9 (n=9)	13.9 (±2.6)	-16.6 (±0.5)	P9 (n=24)	12.9 (±1.5)	-16.5 (±0.6)
	Tristan/ Nightingale	P1 (n=4)	13.9 (±0.9)	-17.1 (±0.2)	P2 (n=20)	11.7 (±2.0)	-16.8 (±0.8)
		P5 (n=3)	14.9 (±0.5)	-17.2 (±0.1)	P5 (n=20)	12.4 (±2.1)	-16.6 (±0.8)
		P9 (n=3)	14.5 (±1.1)	-16.0 (±0.7)	P9 (n=20)	14.4 (±1.4)	-16.5 (±0.3)
	Grouped	P1 (n=13)	11.1 (±2.7)	-17.7 (±0.6)	P2 (n=44)	11.5 (±2.0)	-16.8 (±0.8)
		P5 (n=12)	12.8 (±1.9)	-17.0 (±0.7)	P5 (n=44)	12.3 (±1.8)	-16.5 (±0.7)
		P9 (n=12)	14.1 (±2.3)	-16.5 (±0.6)	P9 (n=44)	13.6 (±1.6)	-16.5 (±0.5)
P. macgillivrayi	Gough	P1 (n=8)	14.2 (±1.7)	-16.6 (±0.4)	P2 (n=24)	14.7 (±0.8)	-16.5 (±0.8)
		P5 (n=8)	13.9 (±2.3)	-16.1 (±0.3)	P5 (n=24)	14.5 (±0.8)	-16.6 (±0.5)
		P9 (n=8)	12.7 (±1.4)	-17.0 (±0.9)	P9 (n=24)	13.5 (±1.1)	-17.1 (±0.5)

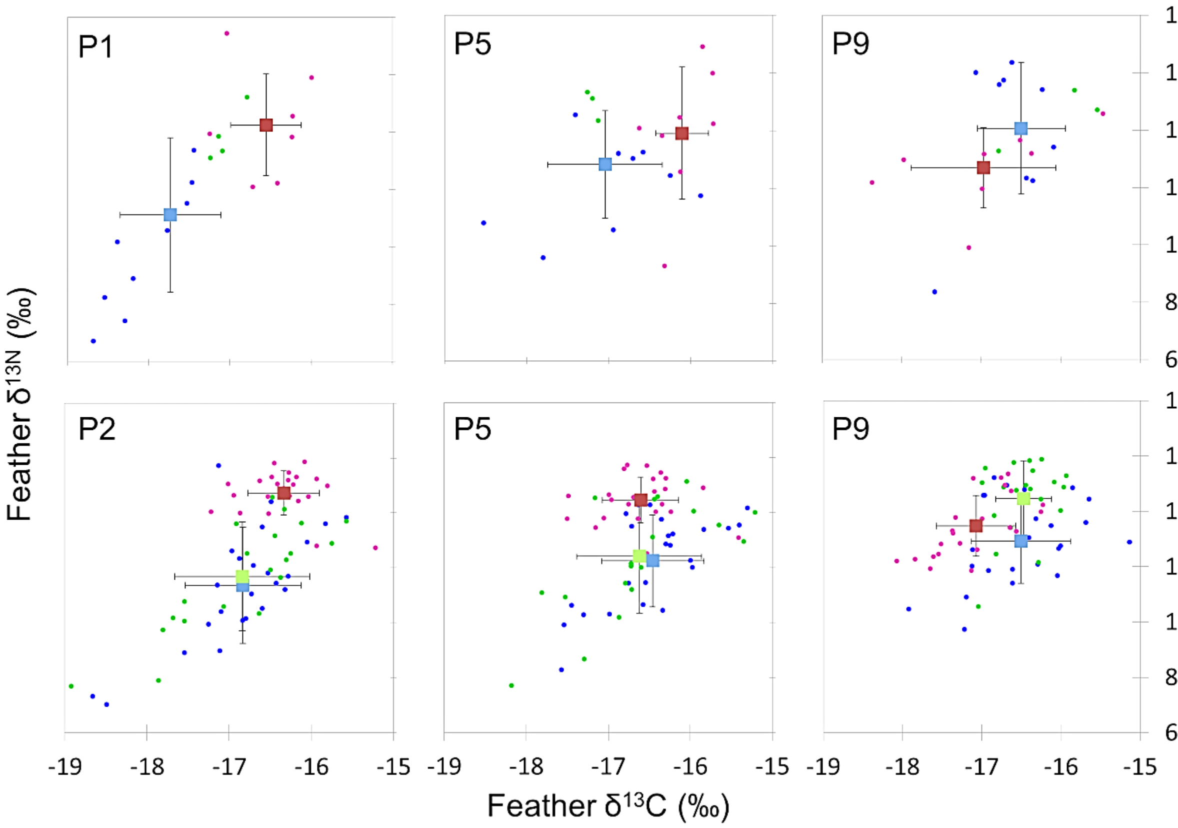

Figure 3.4. Primary feather (P1/2, P5, P9) δ^{13}C and δ^{15}N values of *P. vittata* from Gough (blue), Tristan/Nightingale (green) and *P. macgillivrayi* (red) that were equipped with miniaturized saltwater immersion geolocators in 2015 (top row) and dead birds collected in 2013 (bottom row). Dots are individuals and squares are group means ± SD of species (top row) and populations (bottom row).

Habitat preferences

Habitat preference during the non-breeding season differed between *P. macgillivrayi* and *P. vittata*; the top-ranking model retained a species interaction for distance from the breeding colony, chlorophyll *a*, sea surface temperature and distance to seamount, but not for water depth (**Table 3.6**). Both species showed a preference for waters around 4000 m deep (**Figure 3.5**), with *P. macgillivrayi* moving to waters approximately 2500 km from Gough Island, while *vittata* also used waters closer to their breeding colonies. There was a difference in the preference for productivity between the two species; *P. vitatta* tended to occur in waters with low chlorophyll concentrations, whereas *P. macgillivrayi* occupied waters with a broader range of productivity. *Pachyptila vittata* showed a stronger response to water temperature and had a preference for waters between 15 and 20°C, while *P. macgillivrayi* had a preference for warmer waters (20 - 25°C). Neither species showed any biologically significant selection for areas close to seamounts (**Figure 3.6**).

Table 3.6. Model selection table examining differences between *P. vittata* and *P. macgillivrayi* in preference for distance to colony (DIS), depth (DEP), chlorophyll *a* (CHL), sea surface temperature (SST) and distance to seamount (SEA). Terms in bold indicate the model includes a species-level interaction for that covariate. All models include an individual-level random effect. Adj-R^2 of best-supported model = 0.67.

	Parameters	**d.f.**	**AIC**	**ΔAIC**
1	**DIS** + DEP + **CHL** + **SST** + **SEA**	55.28	7821	0
2	**DIS** + **DEP** + **CHL** + **SST** + **SEA**	59.25	7823	2.52
3	DIS + **DEP** + **CHL** + **SST** + **SEA**	54.98	7879	58.36
4	**DIS** + **DEP** + **CHL** + SST + **SEA**	56.09	7936	115.40
5	**DIS** + **DEP** + CHL + **SST** + **SEA**	52.29	7945	124.01
6	**DIS** + **DEP** + **CHL** + **SST** + SEA	52.88	8053	232.47

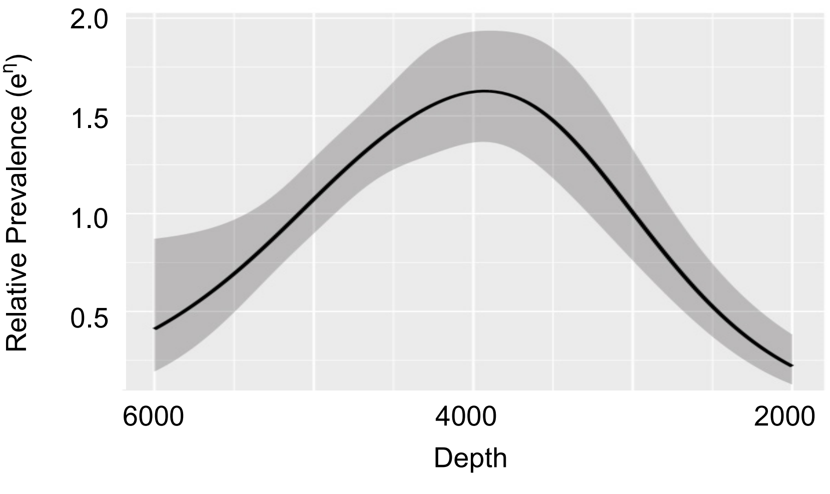

Figure 3.5. Modelled relationship between depth and the equal presence of both *P. vittata* and *P. macgillivrayi* in the non-breeding area. Solid line shows the probability of occurrence; darker grey shaded area shows 95 % confidence intervals.

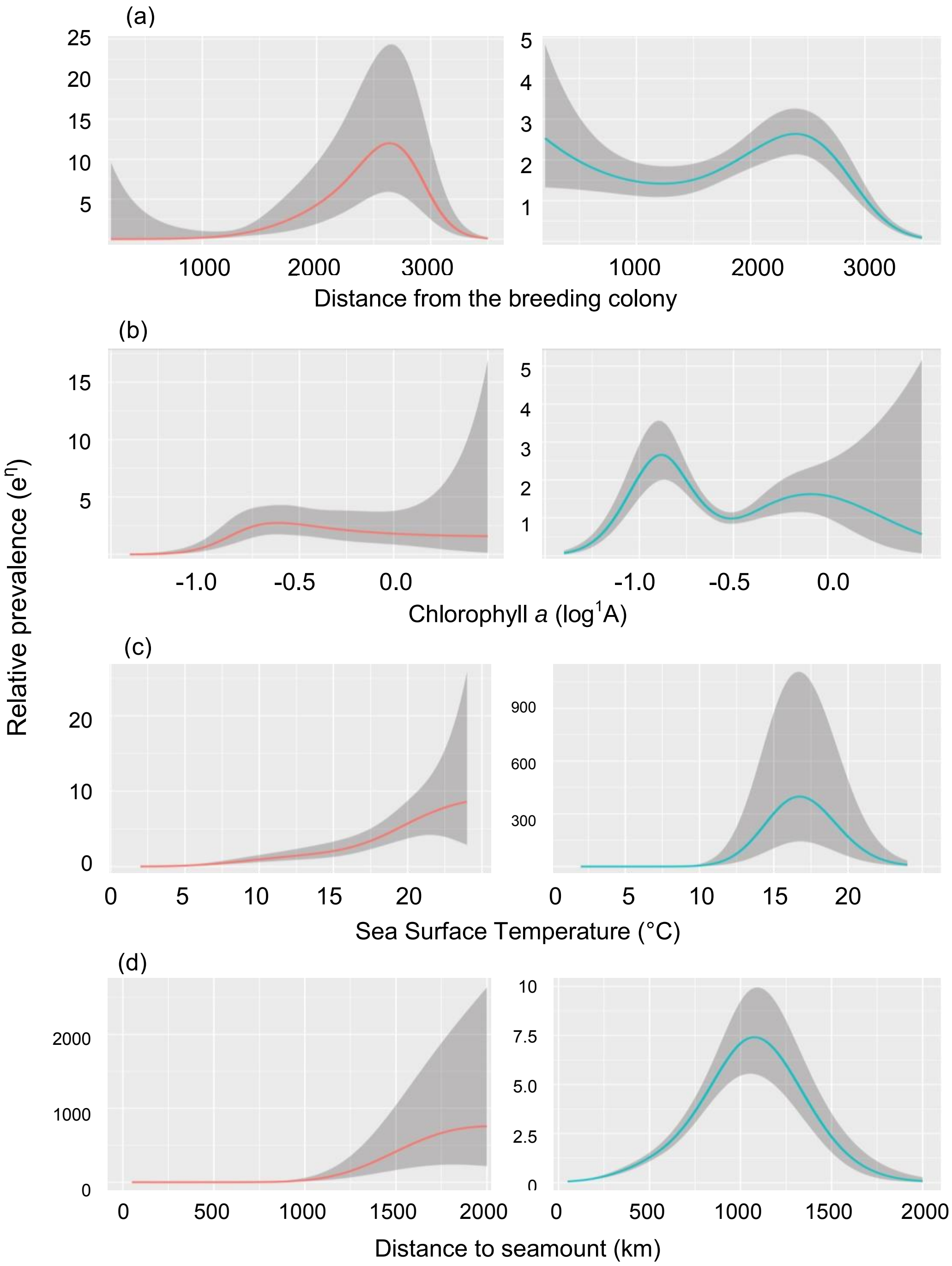

Figure 3.6. Modelled relationships between standardised environmental variables; (a) distance to colony; (b) chlorophyll *a*; (c) Sea Surface Temperature; and (d) distance to seamount, and the presence of P. *vittata* (blue) and *P. macgillivrayi* (red) in the non-breeding area. Solid line shows the probability of occurrence; darker grey shaded area shows 95 % confidence intervals.

DISCUSSION

This is the first study of the spatial distribution, flight patterns and habitat preference of prions from Tristan da Cunha and Gough Island. Together with the stable isotope analysis, it adds to the few studies that have investigated the foraging strategies and ecological segregation across discrete stages of their annual movements (Hedd et al. 2012; Gutowsky et al. 2014 Orben et al. 2015; Cherel et al. 2016). The use of activity data allowed novel insights into the timing of moult in adult prions. The relatively low logger recovery rate, attributed to a combination of complex burrow structure and logistical restraints in revisiting the deployment site at Tristan da Cunha was the main reason for small sample size. However, tracking studies of this type are often associated with modest sample sizes (Phillips et al. 2007b; Navarro et al. 2013; 2015; Quillfeldt et al. 2013). The similarity in feather isotope signatures of the tracked birds and a larger sample of opportunistically sampled birds indicate that each species likely used the same water masses and maintained a similar diet during the moulting period over several seasons. In addition, the proportionate mass of the logger (<1% of body mass) was well below the level (c. 3%) generally thought to affect flight ability (Phillips et al. 2003). It is unlikely therefore that the behaviour of these individuals was compromised by the loggers and presumably, the distribution and activity patterns are typical of the species. Several pelagic seabird species tracked using GLS devices have shown similar patterns of consistent winter distribution, a characteristic that is shared among many seabirds (Croxall et al. 2005; Phillips et al. 2005; 2006; 2007a).

Like Cherel et al. (2016) I found that prions showed a period of marked reduction in flight activity, consistent with the period of intense flight feather moult. Cherel et al. (2016) confirmed rapid post-breeding moult in *H. caerulea*, by matching up activity data with observations of birds at breeding colonies with fresh flight feathers and subsequently inferring timing of moult using with activity data for *P. desolata* and *P. belcheri.* Interestingly *P. belcheri* also undergoes a rapid post-breeding moult, but *P. desolata* migrate to sub-tropical waters first and then have a more protracted moult ending just before they return to their colonies. Neither species returns to the colony during the non-breeding period, unlike *H. caerulea,* which have a schedule similar to *P. vittata* and *P. macgillivrayi* of rapid post-breeding moult followed by a brief return to the colony.

Interestingly *P. vittata* from Tristan departed from and arrived at the breeding colony significantly later than their Gough Island counterparts. The departure of *P. vittata* from Gough Island is closely timed with the return of *P. macgillivrayi* starting their breeding season with little overlap occurring. This difference in phenology between *P. vittata* populations could be a result of character displacement by *P. macgillivrayi*, a characteristic seen in seabirds occupying similar habitat at breeding grounds (Sullivan and Wilson 2001; Friesen et al. 2007; Navarro et al. 2013; Quillfeldt et al. 2015b; Taylor and Friesen 2017). Another explanation could be that all of the *P. vittata* deployed on at Gough Island were unsuccessful breeders with most failures occurring during incubation (September – October), leading to a premature departure from this colony. While deployments at Tristan occurred during the chick brooding stage (4 November), however it is unknown whether any of the Tristan *P. vittata* were successful breeders since the colony was not monitored after deployments. Nonetheless, GLS data suggest significant difference between both populations in all discrete stages of the yearly cycle (departure, moult, arrival, see **Table 3.2**) which is supportive of the character displacement hypothesis.

Although the two prion species at Gough Island are similar in size and presumably feeding methods (Klages and Cooper 1992; Ryan et al. 2014), there was a high degree of inter-specific spatial segregation in core ranges (50% UDs), although more overlap in increasingly peripheral sections of their distributions (**Figure 3.1 and 3.2**). As seen in previous studies, the high mobility of closely-related small petrels facilitates their spatial segregation away from their breeding grounds (Quillfeldt et al. 2013; 2015b; Navarro et al. 2013; 2015; Cherel et al. 2016). Thus, in winter, spatial segregation is one characteristic that allows the coexistence of these two species. Non-breeding *P. macgillivrayi* mainly occurred far west of Gough Island within the Argentine Basin in sub-Antarctic and mixed sub-Antarctic/sub-tropical waters, with distribution extending from the Antarctic Polar Front (APF) to the edge of the Sub-tropical Convergence (STC). Zones within this oceanic region are thought to be productive areas because of eddies created by the Brazil Current and the offshore edge of the Falklands Current (Phillips et al. 2007b). In contrast, *P. vittata* occupied waters to the north and east of *P. macgillivrayi*'s core range, in waters north of the sub-tropical convergence. *Pachyptila vittata* has a wider longitudinal range than *P. macgillivrayi*, showing some movement to the south east Atlantic, in a broadly similar area described as productive, likely in terms of prey concentration, for seabirds in previous tracking studies (Quillfeldt et al. 2013; 2015a; Cherel et al. 2016).

Ecological segregation such as species targeting specific foraging areas (Frere et al. 2008; Navarro et al. 2009; Wilson 2010), diving depths (Mori and Boyd 2004; Masello et al. 2010; Wilson 2010), a difference in diet (Baltz et al. 1979; Ridoux 1994; Weiss et al. 2009), divergent foraging patterns (Wilson 2010) and temporal segregation in timing of activities (Croxall and Prince 1980; Friesen et al. 2017), is thought to alleviate competition in seabirds. However, it is often difficult to determine whether these mechanisms that allow similar species to coexist, is a result of competitive exclusion or habitat specialization. This study shows that two closely related seabird species segregate in several aspects of their ecology, since little overlap is seen in: trophic level of diet (at least during the moult period, inferred from feather δ^{15}N isotopic signatures, diurnal foraging strategies suggested from flight patterns (**Table 3.4**) and breeding chronology. Therefore, the contrasting spatial distribution between the species points towards habitat segregation in regions specific to each species.

The differences in spatial distribution and habitat preferences, mainly in terms of sea surface temperature and chlorophyll *a*, of the two species suggest an element of niche specialisation; this was also reflected in different non-breeding activity patterns outside the moult period. Compared to *P. vittata*, *P. macgillivrayi* spent a significantly greater proportion of both daylight and darkness, and more hours on average, in flight, indicative of greater search effort and consistent with the higher trophic level at which it feeds. Phenology may be one of the factors influencing the differences in habitat preferences and foraging ecology. Seasonality of resources and productivity in the Southern Ocean are well documented (Pakhomov and McQuaid 1996; Llido et al. 2005; Bost et al. 2009). *Pachyptila macgillivrayi* moults on average 78 days later than *P. vittata*, during early winter, so may have to spend more time searching for food. The longer duration of moult in *P. macgillivrayi* also suggests that resources may be more limited at this time. Primary feathers have a uniform growth rate in birds (Bridge 2006), suggesting prions with a shorter moult were able to meet the energetic demands of replacing feathers, even when flying ability was compromised (Cherel et al. 2016). The longer moult period in *P. macgillivrayi* probably is a result of moulting fewer feathers at once, which is consistent with spending more time in flight throughout moult (**Table 3.4**).

In conclusion, the two prion species achieve near complete ecological segregation through a combination of spatial, temporal and trophic segregation. This study furthers the understanding of how morphologically similar species coexist at high abundances. The tracking data have allowed habitat preferences and key foraging areas for these species to be identified. This will assist with marine spatial planning, allowing informed decisions regarding the mitigation of climate driven impacts on zooplankton communities (Grecian et al. 2016).

Supplementary material

Table S3.1. Comparative bill morphology of three filter-feeding prion species The number of palatal lamellae represents the average the number counted on the left and right sides of the bill. Values are means ± SD. Values not sharing the same superscript letter are significantly different at the 0.05 level (ANOVA, with posthoc Newman–Keuls tests).

	P. vittata (n = 30)	*P. macgillivrayi* (n = 30)	*P. salvini* (n = 23)	ANOVA results
Bill width (mm)	22.2 (±1.0)^a	18.5 (±0.8)^b	16.4 (±0.8)^c	$F_{2, 82}$=287.8, p<0.001
Bill length (mm)	34.2 (±1.3)^a	33.3 (±1.4)^b	30.1 (±1.7)^c	$F_{2, 82}$=56.7, p<0.001
No. of Lamellae	132 (±9)^a	119 (±10)^b	106 (±12)^c	$F_{2, 82}$=38.0, p<0.001
Lamellae/mm	3.3 (±0.3)	3.4 (±0.2)	3.4 (±0.2)	$F_{2, 82}$= 0.4, p=0.692

Table S3.2. Breeding success comparison of *Pachyptila* spp. monitored on Gough Island in 2014/15. GLS represents nest where either one or both partners were tagged with geolocator loggers.

		Failure		Chicks fledged
		Incubation	Chick rearing	
P. macgillivrayi	Control (n=44)	59%	41%	0%
	GLS (n=15)	53%	47%	0%
P. vittata	GLS (n=11)	55%	45%	0%

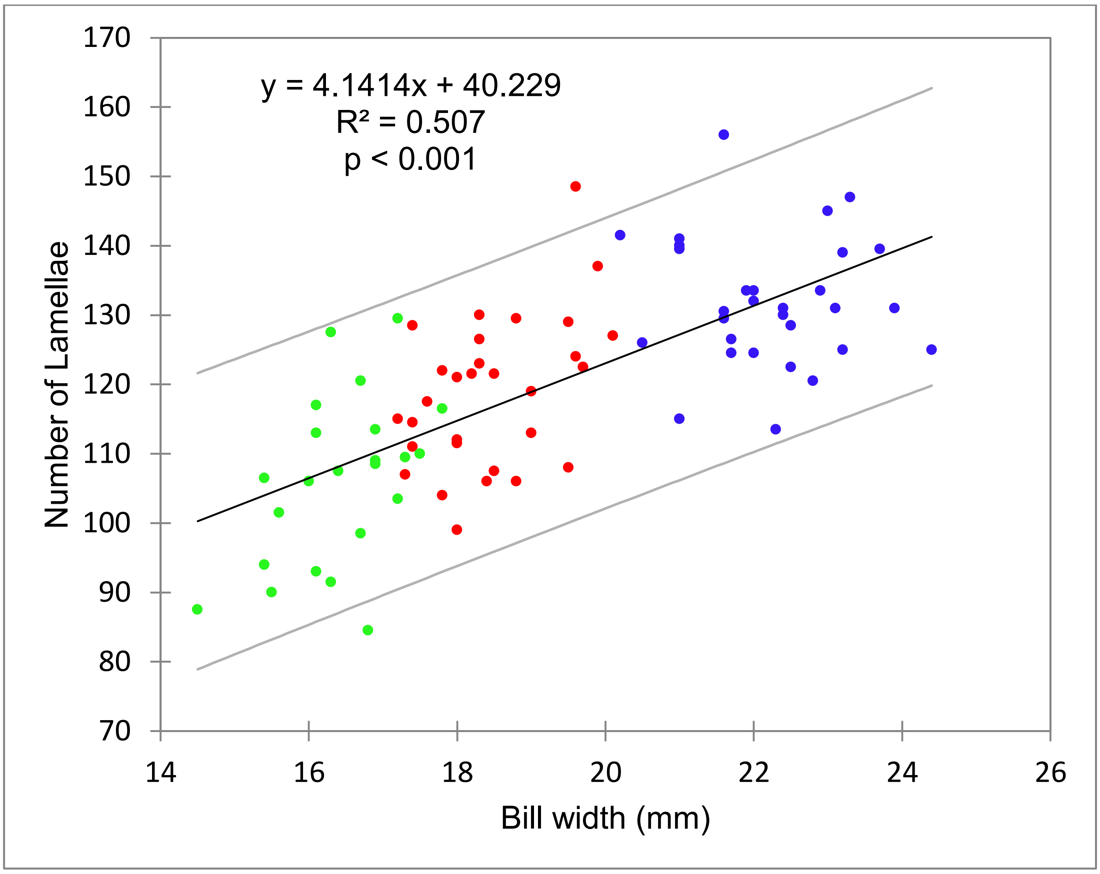

Figure S3.1. Comparison of the relationships between bill width (mm) and number of average number of palatal lamellae based on counts of the left and right sides of the upper mandible from a sample of dead specimens. Data from *P. salvini* (green, n=33), *P. macgillivrayi* (red, n=30) and *P. vittata* (blue, n=30) are combined. Regression parameters are given along with 95% prediction limits (grey lines), coefficients of determination (R^2) and level of statistical significance (p).

Chapter 4

Synthesis and conclusions

This chapter discusses the significance of the findings, and combines the ideas presented in the thesis to produce a fresh understanding of the ecology of *Pachyptila vittata* and *P. macgillivrayi*. The chapter concludes with suggestions for future research.

Purpose of the study

This thesis investigated the comparative ecology of the two prion species breeding sympatrically on Gough Island. This is important when considering the similarity in population sizes of the two species at Gough Island (Chapter 2) and mechanisms of segregation throughout their annual cycle (Chapter 3). The principal motivation for the study was based on the premise that there were no tracking data for these species and a limited understanding of their nesting distributions. The research was also carried out to obtain a broader picture of how two closely related and very abundant species adjust their niches to limit inter-specific competition. Pelagic seabirds exploit large areas of ocean when acting as central-place foragers during the breeding season, and their ranges are even more extensive outside the breeding period. Niche partitioning has been shown to occur in several ways among species during the breeding period of sympatric species (Navarro et al. 2015; Quillfeldt et al. 2015b), but may have different drivers in the non-breeding period when there is increased potential for overlap among closely related species from neighbouring island groups (Navarro et al. 2013; Quillfeldt et al. 2013; 2015a; Clay et al. 2016). As the prions are ecologically similar, studies of their spatial coexistence have been important in understanding ecological segregation and how seabird communities assemble (Navarro et al. 2013; 2015; Quillfeldt et al. 2013; 2015b; 2015a; Cherel et al. 2016).

Key Findings

The thesis provides the first tracking information of these two species of prion breeding on Gough Island and adds to a growing number of studies tracking small petrels to further understand their movements in relation to environmental change (Quillfeldt et al. 2010; Cherel et al. 2014; Grecian et al. 2016). In addition, this thesis adds valuable knowledge about the relative population sizes of these difficult to census burrowing species that have recently been shown to be at risk of several conservation threats.

Chapter 2 reported the nesting distribution of *P. vittata* and *P. macgillivrayi* and updated population estimates for these species on Gough Island. It confirmed the conclusions drawn by Ryan et al. (2014) and extended this to show that the two prion species exhibit local allopatry on an island wide-scale. However, I also found a small amount of sympatric breeding on a local scale, which indicates that both species are able to occupy similar nesting habitat. In light of this, it is possible that such clear patterns of spatial segregation are possibly due to the earlier breeding *P. vittata* largely avoiding habitats preferred by *P. macgillivrayi* in order to reduce competition during the overlap in breeding seasons. This hypothesis is further supported by the indication of character displacement between the two species, revealed in phenology determined from GLS data (Chapter 3). Importantly this Chapter also highlighted that the previous population size posited for *P. macgillivrayi* was conservative, confirming the importance of Gough Island as the most important breeding site for both species, and especially *P. macgillivrayi*.

Chapter 3 used complementary methods to examine the foraging ecology, trophic level and oceanic habitat preferences of the two prion species, giving valuable insights into the mechanisms that allow these two abundant prions to coexist. Due to the three month difference in the onset of breeding at Gough Island, spatiotemporal overlap of foraging areas is minimal for most of the annual cycle. Spatial overlap is highest when temporal overlap is highest i.e. when *P. macgillivrayi* return to the colony in October and November before their pre-lay exodus, coinciding with the breeding period of *P. vittata* as well as in May and June when *P. macgillivrayi* return to Gough after completing moult while *P. vittata* are departing after their post-moult reoccupation of burrows. Similar movement patterns and habitat preferences of these prions are observed during the interbreeding period, when both species forage mainly within the Argentine Basin to the west of the breeding islands. This makes the temporal difference in timing of activities crucial to reducing spatial overlap. An interesting finding related to temporal separation is the earlier departure and onset of breeding exhibited by *P. vittata* from Gough Island in comparison to their Tristan counterparts, possibly explained by character displacement in the presence of *P. macgillivrayi*.

In the broader context of resource segregation, it appears that differences in foraging equipment might relate to differences in trophic niche. Given that the spacing between palatal lamellae differs insignificantly between species (**Table S3.1**, Klages and Cooper 1992), both species likely feed on similar-sized copepods. The slightly narrower bill of *P. macgillivrayi* has fewer palatal lamellae on average, and is likely less efficient at filtering and more efficient at surface-picking for food. This is consistent with the greater time spent in flight by *P. macgillivrayi*, perhaps searching for larger prey. However there does not appear to be a relationship between bill width and trophic level when comparing with isotopic data from *P. desolata* and *P. belcheri* breeding at the Kerguelen archipelago (**Table 4.1**). However there appears be a relationship between trophic level and duration of moult. $\delta^{15}N$ is higher in prion species that take longer to moult. By spending more time on water, perhaps *P. desolata* and *P. belcheri* use an opportunistic sit-and-wait foraging strategy by picking out low trophic prey items in highly productive foraging areas. In comparison, *P. vittata* occupy a higher trophic level maybe because they are unable to select what their lamellae pick up and *P. macgillivrayi* occupies the highest trophic level of these four prion species by using a combination strategy of picking out prey and filtering-feeding.

Table 4.1. Summary of flight patterns and trophic level ($\delta^{15}N$) in comparison with bill morphology and duration of moult. Data for *P. desolata* and *P. belcheri* are from Cherel et al. (2016). Species limits are given for bill width and other values are means ± SD.

Species	Bill width (mm)	Moult duration (days)	Flight time (%)		$\delta^{15}N$ (‰)
			Non-moulting	Moulting	
P. vittata	20-24.5	95±8	44±6	20±3	12.6±2.0
P. macgillivrayi	15.5-20.5	115±10	53±3	24±5	13.9±1.4
P. desolata	12-16	109±13	28±7	17±9	11.4±2.0
P. belcheri	9-12	83±13	24±3	5±2	8.8±0.4

Another important finding to consider is habitat preferences indicated by the habitat models produced from tracking data. Unlike in the south Pacific (Grecian et al. 2016), neither *P. vittata* nor *P. macgillivrayi* was found to have a biologically meaningful response to seamounts over their foraging range. Thus as suggested by Torres et al. (2015), broad inferences in target areas for marine spatial planning are not necessarily transferable over ocean basins.

Implications of the findings and suggestions for future research

The distribution of the nesting populations of prions at Gough Island needs to be empirically related to habitat features, in order to better understand if land-based factors could limit their distribution and abundance. Quantifying physical features and understanding habitat selection of both species can assist future management in order to maintain healthy populations (Stokes and Boersma 1991). Although Gough Island is the most important breeding site for these *Pachyptila* species and dedicated ornithological research has been conducted at this site since 2008, a thorough and repeatable census is yet to be attempted. Population estimates of both species are required to provide a better indication of the importance of this site for these species, and to provide baseline data for future assessment and monitoring. The large number of birds, relatively wide distribution, and occurrence of communal burrows as well as cave breeding sites at Gough Island means a methodology based on standard burrow counts and occupancy scores (e.g. Catry et al. 2003, Cuthbert 2004) may be unsuitable. However, monitoring nest occupancy at selected habitat types may be useful as a proxy for detecting change in population trends.

The tracking component of this thesis was perforce based on a small sample of individuals, constrained further by low device recovery rates. Although the sample size is similar to several other GLS studies of small petrels (e.g. Navarro et al. 2013; 2015; Quillfeldt et al. 2013; 2015b; 2015a), and a larger sample of birds for stable isotope analysis was used to supplement the tracking data, it would be beneficial to aim for larger sample sizes in future studies of this nature. It would also be interesting to track the same individuals in successive years to assess how individuals respond to environmental variability (cf. Croxall et al. 2005; Phillips et al. 2005; 2006; Guilford et al. 2011; Thiebot et al. 2011; Yamamoto et al. 2014; Quillfeldt et al. 2014; 2015a; 2015b; Carneiro et al. 2016). Birds tracked in this study were individually tagged with rings, so continued monitoring at the deployment site should be done in order to keep a record of individual histories, which may reveal more details on information gained from the current tracking data as well as identify priorities for potential future tracking device deployments. There was an element of variation within species with regard to at-sea distribution; further investigation of such variation is likely to increase our ability in making sound conclusions on animal movement (Hawkes 2009).

Seabirds have been shown to exhibit foraging behaviour plasticity under a changing environment, thus large-scale regime shifts may result in prions having to adapt to a new environment that could carry substantial energetic and evolutionary costs (Kappes et al. 2010; Grecian et al. 2016). Many seabird populations have decreased dramatically in the last century, which has been attributed to a number of processes that threaten their survival (Croxall et al. 2012). The desire to use these seabirds as bio-indicators of marine resources and pollution has prompted to these animals being studied extensively. However, if we are to use the foraging behaviour and population trends of prions to improve our understanding of the marine environment, their breeding sites need to be preserved. This provides further motivation to eradicate invasive house mice from Gough Island (Cuthbert et al. 2013; Dilley et al. 2015).

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