Does size matter?

Sex differences in white-faced storm petrels’ ecology

by

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I am the author of the thesis entitled

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Abstract

Differences between the sexes are common in a wide range of species and can greatly influence their ecology. The Procellariiformes (albatrosses, petrels and shearwaters) are a unique order of seabirds that exhibit varying degrees of sexual size dimorphism (SSD), both male-biased and female-biased. Our review of the Procellariiformes found that the direction of SSD in measures of body size (tarsus, wing and tail lengths), changes from male-biased in the larger species to female-biased in the smaller species, whilst bill dimorphism remains male-biased. In the smaller species, such as the white-faced storm petrel (*Pelagodroma marina*), females are 0.95% - 2.76% larger than males in measures of body size. However, males have significantly larger bill depths (1.7%). In addition, we found that these patterns of SSD are also present in white-faced storm petrel offspring prior to fledging.

Whilst differences in SSD in the white-faced storm petrel are minute they may influence the biology and ecology of this species. We found no sex differences in the growth rates, meal sizes or provisioning rates of white-faced storm petrel chicks, suggesting that the differences in SSD do not result in extra energetic costs to parents in raising a particular sex. However, we did find differences in the foraging behaviour of male and female adult white-faced storm petrels throughout the breeding period. During chick rearing male white-faced storm petrels spent a greater proportion of time undertaking short foraging trips, while females undertook a greater proportion of time undertaking long foraging trips. We suggest that these differences in foraging behaviour may be a result of differences in SSD of white-faced storm petrels, where bill size may influence diet and body size potentially influences flight ability and territorial defences. This may lead to segregation in foraging distributions and have implications for parental investment.

We investigated differences between two geographically distant white-faced storm petrel colonies being Mud Islands in Port Phillip Bay and Tullaberga Island in the far east of Victoria, Australia. Crustaceans and fish represented a high proportion of the white-faced storm petrels’ diets at both locations with coastal krill (*Nyctiphanes australis*) being the most abundant prey item. Differences in the diet between locations and seasons were also recorded suggesting that white-faced storm petrels from each colony are likely to be foraging in different areas. While there was limited difference in diet composition between
male and female white-faced storm petrels, there were differences in the size of prey targeted by each sex, males fed on larger krill than females, while females fed on larger amphipods. This potential segregation in prey size selection may be a result of subtle SSD in bill morphology of white-faced storm petrels and consequently reduced inter-specific competition for resources.

Little information is available on the migratory behaviour and non-breeding distributions of white-faced storm petrels from both Mud Islands and Tullaberga Island. Understanding of the year-round distribution is an important aspect of a migratory species ecology and essential for their conservation. Stable isotope analysis of feathers revealed significant variation in $\delta^{13}$C values from white-faced storm petrels from the two breeding colonies. The results provide evidence of potential segregation of moulting and therefore wintering grounds (i.e. a migratory divide) for white-faced storm petrels from Mud Islands and Tullaberga Island. Also here we found intersexual differences in $\delta^{15}$N values in white-faced storm petrels suggesting differences in trophic level and thus diet between the sexes.

Overall, we find that size does matter and that even subtle SSD impacts the biology and ecology of the white-faced storm petrel, attributing to the ecological implications of SSD across the entire order of Procellariiformes.
This thesis has been written with a view to publishing all data chapters (Chapters 2 – 5) as stand-alone manuscripts. As such, there is some overlap and repetition in the introduction and methods sections of some chapters. I am the principal contributor of all chapters in this thesis, and will be the primary author on all publications arising from this research.

All work was conducted under Deakin University Animal Ethics Committee approval (A25/2005, A26/2006, A27/2006, and A35/2006) and research permits issued by the Department of Sustainability and Environment (1003129) Victoria. All bird bands were supplied by the Australian Bird and Bat Banding Study (Authority 2536 - Project No. 1).

All volunteer field assistants collected data under my supervision. These volunteers provided assistance with fieldwork however they played no part in the analysis or interpretation of results. Additional expertise was required for analysis for some parts of this thesis. In Chapter 2 analysis of blood samples to determine the sex of individuals was undertaken by Ashley Herrod at Monash University and also by Genetic Technologies, Melbourne. The analysis of staple isotope ratios of $\delta^{13}$C and $\delta^{15}$N were analysed at the Environment Biology Group Stable Isotope Facility, School of Biological Sciences, Australian National University. Caroline Wilson undertook some of the nightly weighings of chicks for meal size (Chapter 3). Nicole Schumann assisted with initial identification of prey items found in diet samples, provided assistance on analysis and provided critical evaluation of a draft (Chapter 4), and will be a co-author of that publication. Further identification of prey items was undertaken by Dr Wolfgang Zeidler from the South Australian Museum and Dr Shane Ahyong from the Australian Museum. Professor Marcel Klaassen will be co-author on all publications arising from this thesis as he has assisted with analysis, provided advice and critical evaluation of drafts throughout this research.
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'Too due list' - Piled Higher and Deeper" by Jorge Cham
www.phdcomics.com
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Chapter 1

GENERAL INTRODUCTION
Chapter 1 – General introduction

The difference between the sexes

Differences between the sexes are found throughout both the plant and animal kingdoms. These differences can be in the behaviour, morphology, or physiology of an individual organism. Some of these differences are obvious while others are more discreet. Nevertheless, these differences have evolved in species and are likely to play an important role in their ecology.

The primary purpose of most differences between the sexes can generally be related to breeding ecology. Body size can be an important aspect for competition between males in order to establish and defend a territory for breeding. For example, older, larger elephant seals *Mirounga* sp. have higher breeding success as they are able to prevent the younger, smaller males from copulating with females (Andersson 1994). Ornamentation, such as the brightly coloured plumage of the superb fairy wren (*Malurus cyaneus*), can be essential for mate acquisition (Mulder & Magrath 1994). In some species differences between the sexes can play an important functional role for reproduction, for example, a large claw may be necessary to hold a female in position to mate successfully (Reynolds & Harvey 1994). In addition, differences between the sexes may occur in order to reduce competition within a species (Selander 1966). For example, in woodpeckers (*Centurus* sp.), sexual differences in bill length have resulted in variation in the types and frequency of a sex utilising specific foraging techniques and consequently suggests differences in foraging locations (Selander 1966). Again, some of these differences are extreme while others can be more subtle; however, they still serve an important purpose in the evolution and adaptation in individuals, species and groups.

Sexual size dimorphism (SSD) is common throughout a range of species and can be either male-biased, where males are larger than females, or female-biased where females are the larger sex. In many species of birds the males are frequently larger than females with a few exceptions where female-biased SSD exists (e.g. some raptors, owls, shorebirds and seabirds; Jehl & Murray 1986, Fairbairn & Shine 1993). Three hypotheses are commonly used to describe the evolution of SSD being: sexual selection hypothesis, intersexual niche divergence hypothesis, and the dimorphic niche hypothesis (Hedrick and Temeles 1989).
Firstly, Darwin (1871) proposed the theory of sexual selection evolves when specific characteristics are selected for in a particular sex where they provide an advantage in either competition for mates and mate selection. Secondly, the inter-sexual niche divergence hypothesis (also referred to as the ecological sexual dimorphism hypothesis) suggests that differences between the sexes evolve to reduce interspecific competition for food and foraging resources (Selander 1966). Finally, the dimorphic niche hypothesis (also referred to as the reproductive or fecundity selection hypothesis) states that sexual dimorphism results from differences in the reproductive roles or parental investment of the sexes (Fairbairn 1997). Studies of SSD in a range of species have revealed differences between the sexes in various aspects of their ecology that can be related to one or more of these hypotheses (Hedrick & Temeles 1989). However, it can be difficult to discern the relative importance of each hypothesis and the degree to which each may explain the selection for SSD within a species (Hedrick & Temeles 1989).

The Procellariiformes

The Procellariiformes (albatrosses, petrels, shearwaters and storm petrels) are an order of seabirds that range in body size from 19.5 g in the smallest of the storm petrels to over 8500 g in the largest of the albatrosses (Warham 1990). Individuals within each species are generally indistinguishable in terms of plumage. However, there are often differences in morphology (Warham 1990). Procellariiformes are unique order of seabirds, in that they exhibit SSD that can be male-biased or female-biased. The degree of SSD also varies considerably, amongst the larger species, such as the giant petrels, there are obvious differences with males being significantly larger in overall body size than females, whilst in the smaller storm petrels the differences are more subtle with females only slightly larger than males (Fairbairn & Shine 1993, Warham 1990).

The direction and degree of sex differences in biology and ecology vary between different species throughout the Procellariiformes. Procellariiformes have developed specific strategies to cope with the unpredictability and patchiness of the marine environment (Lack 1968). All species within this order lay only a single egg and have extended incubation and chick rearing periods and both sexes contribute to the incubation and chick rearing (Warham 1990).
Despite these similarities in life history traits exhibited in Procellariiformes, the direction and degree of SSD varies (Warham 1990). For example; in some of the larger species differences between the sexes have been found in diet (González-Solis 2004), foraging areas (González-Solis 2007), parental investment (Quillfeldt et al. 2004), and migratory distributions (Phillips et al. 2009). Further examples are provided in the following data chapters. In many cases these variations between the sexes has been attributed to differences in morphology. However, in the smaller Procellariiformes, little data is available that investigates how SSD affects the ecology of the sexes.

**White-faced storm petrel (Pelagodroma marina)**

The smallest members of the Procellariiformes, the storm petrels, exhibit reversed sexual size dimorphism in body size (Warham 1990). Although differences in SSD in storm petrels tend to be minute, they still have the potential to influence the ecology of the species. The white-faced storm petrel (*Pelagodroma marina*, Latham 1790) is a small storm petrel (50 – 70 g; Marchant & Higgins 1990), comprising six subspecies, found in both the northern and southern hemispheres. Few studies of the white-faced storm petrel have been undertaken. Richdale (1943 & 1965) studied the New Zealand subspecies, *P. marina maoriana*, at Whero Island from 1940 – 1945. In addition, the breeding biology of the European subspecies, *Pelagodroma marina marina*, was studied over a single season during 1996 (Campos & Granadeiro 1999). In Australia, extensive banding of *P. marina dulciae* was undertaken almost annually at Mud Islands from 1955 – 1980, with over 12,500 individuals banded, although only 2% were recovered with most recaptures at Mud Islands (Menkhorst et al. 1984).

In Australia, the white-faced storm petrel is found on many offshore islands from Abrolhos Islands, Western Australia, south through to Broughton Island, New South Wales (Serventy et al. 1971). The white-faced storm petrel nests in long shallow burrows with adults returning to the colony after dark. As with other Procellariiformes they lay a single large egg and have an extended incubation and chick rearing period (Warham 1990). The white-faced storm petrels are present at the breeding colony during the austral summer from late August until March (Underwood & Bunce 2004). Eggs are laid from late October and incubated for approximately
50 days, with chicks hatching from December and chicks fledging approximately 55 days later (Underwood & Bunce 2004). Limited information on white-faced storm petrel diet has shown that it predominately consists of pelagic crustaceans, small fish and other surface plankton (Marchant & Higgins 1990). Following the breeding season the white-faced storm petrel migrates to the northern hemisphere. However, little is known about their distributions during the non-breeding period (Imber 1981).

Study sites
In Victoria, the white-faced storm petrel is restricted to three breeding colonies, being Mud Islands and South Channel Fort, both within Port Phillip Bay, and Tullaberga Island in far eastern Victoria (Figure 1.1).

Mud Islands
Mud Islands form part of the great sands within Port Phillip Bay (38°16’30”S, 144°45’00”E, Figure 1.1) and comprises of three separate islands (approx. 60ha) surrounding a central lagoon. The islands also form part of the Port Phillip Heads Marine National Park and are a RAMSAR site. Mud Islands are a dynamic environment that has dramatically changed in shape over time. The islands support breeding populations of more than 14 bird species and are also an important feeding and roosting area for a number of shorebird species. Silver gulls (*Larus novaehollandiae*) were first recorded in the 1970’s and populations have since increased to between 50 – 70,000 pairs (Menkhorst *et al.* 1988). In addition, from the early 1990’s, both the Australian white ibis (*Threskiornis molucca*) and straw-necked ibis (*Threskiornis spinicollis*) were recorded breeding on Mud Islands and have since increased to over 50,000 pairs (personal observations). The vegetation has changed significantly over time with the number of plant species more than tripling, which is likely to be a result of an increase in the numbers of birds breeding on the islands (Yugovic 1998). The population of white-faced storm petrels at Mud Islands have declined from an estimated 22,000 pairs in 1928 to approximately 5,600 pairs in 1978 (reviewed in Menkhorst *et al.* 1984) and less than 2,500 pairs in 2007 (M. Underwood, unpubl. data). These declines are most likely a result of changes in vegetation, competition for breeding areas and the removal of rabbits from Mud Islands.
South Channel Fort

South Channel Fort is a small man-made island (approx. 0.6 ha) located in Port Phillip Bay (38°19'00"S, 144°48'00"E, Figure 1.1). Constructed in the 1880’s as part of the defence strategy to protect the port of Melbourne, it contains a series of underground tunnels and gun emplacements and now forms part of Point Nepean National Park. White-faced storm petrels were first recorded breeding here in the early 1920’s (Harris 1979). The population was estimated at over 6,000 pairs in 1978 (Harris 1979). However, only a small number of storm petrels are currently breeding on the island (M. Underwood, personal observations). The introduced African boxthorn (*Lycium ferocissimum*) had, until recently, taken over much of the island and resulted in a number of white-faced storm petrels and silver gulls becoming impaled on the thorns. A small number of white-faced storm petrels have also been found trapped in the tunnel system or drowned in gun emplacements (Harris 1979). Visitors to the fort have also caused some disturbance to the storm petrel population through trampling of burrows. Other species found breeding on the fort include silver gulls (over 1000 pairs) and a small population of little penguins (*Eudyptula minor*).

Tullaberga Island

Tullaberga Island is a small granite island approximately 3ha in size, located in far east Victoria (37°34’00"S, 149°51’00"E), and forms part of the Croajingolong National Park (Figure 1.1). Tullaberga Islands supports populations of little penguins and short-tailed shearwaters (*Puffinus tenuirostris*). The white-faced storm petrel population was estimated to be over 21,000 pairs in 1978, making it by far the largest colony in Victoria (Harris 1979). It is likely that the population has declined since then and the current status is unknown (M. Underwood, personal observations). The short-tailed shearwater population appears to have since increased and may provide competition with white-faced storm petrels for nesting area (personal observations). Seabird populations are well protected as there is no visitor access permitted on the island.
Figure 1.1 Location of white-faced storm petrel (*Pelagodroma marina*) breeding colonies in Victoria, Australia. Both Mud Islands and South Channel Fort are located in close proximity and are within Port Phillip Bay.

**Thesis objectives and overview**

The main objective of this research is to determine the degree of sexual size dimorphism in white-faced storm petrels and the potential influence these subtle differences may have on a range of aspects of the biology and ecology of male and female white-faced storm petrels. Firstly we review the occurrence of SSD throughout the Procellariiformes in relation to body size. Following which we investigate how SSD in white-faced storm petrels influences the chick growth and provisioning, the foraging behaviour and parental investment of adults, diet and prey size selection and migration of the white-faced storm petrel. This study was conducted across the three Victorian white-faced storm petrel colonies, being Mud Islands,
South Channel Fort and Tullaberga Island. Furthermore we explored two the three hypothesis of SSD in relation to our observations of the white-faced storm petrel. It is unlikely we will be able to determine in evidence for the theory sexual selection in this study. However, the inter-sexual niche divergence and dimorphic niche hypothesis both have the potential to influence SSD in the white-faced storm petrel.

This thesis has been written with the intent to publish each data chapter (Chapters 2 – 6) as standalone manuscripts. Chapter 2 provides a case study of SSD in white-faced storm petrels, following which that data is combined with a broader review of the literature to provide an overview of trends and drivers of SSD in Procellariiformes. Chapter 3 investigates SSD in white-faced storm petrel chicks in terms of the potential energetic costs that can be associated with raising chicks of a particular sex. The chick growth rates, meal sizes and SSD of chicks prior to fledging are explored. Chapter 4 investigates the incubation and foraging behaviour of white-faced storm petrels throughout the breeding season to determine potential variation in parental investment between the sexes. Chapter 5 examines the diet composition between two geographically distant white-faced storm petrels. In addition the size of prey selected and potential niche segregation between the populations and sexes is discussed. Chapter 6 utilises stable isotope analysis in an attempt to differentiate between breeding and hypothesised non-breeding foraging distributions. Potential segregation between the sexes is also examined. Chapter 7 provides a synthesis of the key findings of this research and discusses how these results relate to the theories of sexual size dimorphism in Procellariiformes.
Chapter 1 – General introduction

References


Chapter 1 – General introduction


Chapter 2

Opposing Trends in Size Dependant Sexual Size Dimorphism in Procellariiformes and Their Potential Drivers
Abstract

Differences between the sexes are common in a wide range of species. The degree of sexual size dimorphism (SSD) varies as do the drivers of these differences. In the majority of Procellariiformes SSD occurs and can be male-biased or female-biased. Firstly we conducted a case study on SSD of the small white-faced storm petrel (*Pelagodroma marina*), as there is limited data on SSD in the smaller Procellariiformes. We found that reversed SSD occurs in white-faced storm petrels, with females being significantly larger than males in tarsus, wing, and tail lengths (0.95% – 2.76%). However, males were found to have significantly larger bill depth than females (1.70%). Discriminant function analysis correctly assigned 75% of the female and 68% of the male white-faced storm petrels based on total head length, bill length, bill depth, tarsus length, and wing and tail length. Secondly, we combined these data with those from other Procellariiformes in the literature we found the direction of sexual size dimorphism in measures of body size (tarsus, wing and tail lengths) changes from male-biased to female-biased in the smaller species, whilst bill dimorphism remains male-biased. We discuss the ecological importance of this, variable and sometimes minute, SSD throughout the Procellariiformes.

Introduction

Sexual size dimorphism (SSD) amongst different species can be both male-biased, with males being larger than females, and female-biased, where females are larger than males. In many species of birds the males are frequently larger than females with a few exceptions where female-biased SSD exists (e.g. some raptors, owls, shorebirds and seabirds; Jehl & Murray 1986; Fairbairn & Shine 1993). Generally, in birds, SSD increases with body size in taxa where males are the larger sex; however, in taxa where females are the larger sex this difference becomes more pronounced in smaller species (Rensch’s Rule; Rensch 1966).

There are three hypotheses commonly accepted to describe the evolution of SSD: sexual selection, inter-sexual niche divergence hypothesis, and the dimorphic niche hypothesis (Hedrick and Temeles 1989). Sexual selection was first described by Darwin (1871), proposing that SSD evolves when characters that provide advantage in either competition for mates and
mate selection are selected for in a particular sex. The inter-sexual niche divergence hypothesis (also referred to as the ecological sexual dimorphism hypothesis) suggests that differences between the sexes evolve to reduce interspecific competition in food and foraging (Selander 1966). The dimorphic niche hypothesis (also referred to as the reproductive or fecundity selection) states that sexual dimorphism results from differences between the sexes in their reproductive roles or parental investment (Fairbairn 1997).

In the order Procellariiformes both male-biased and female-biased SSD are exhibited. Species in this order of seabirds range in body size from a mere 19.5 g in the smallest, the least storm petrel (Halocypetra microsoma), to 8700 g in the largest, the royal albatross (Diomedea exulans; Warham 1990). Generally the larger species typically display male-biased SSD while the smaller species exhibit female-biased dimorphism. Variation between the sexes within some species of Procellariiformes have been found to coincide with segregation of foraging areas (Shaffer et al. 2001) and wintering grounds (Phillips et al. 2005), differences in diet (Copello et al. 2006), parental care (Thalmann et al. 2007, Weimerskirch et al. 1997), and vocalisations (Croxall 1982).

Following from these results, all three hypotheses, sexual selection, ecological or dimorphic niche hypothesis, have been used to explain the variation in the degree and direction of SSD in seabirds. Serrano-Meneses & Szekely (2006) review of seabirds supports the sexual selection hypothesis with SSD being correlated to agility of male displays, with males being smaller in species that exhibit aerial displays compared to those that display on the ground where males are larger (compared to females). Differences in flight performance resulting in segregation of foraging areas in albatross has been attributed to the niche divergence hypothesis, with males having a much higher wing loading allowing them to travel further south more efficiently (Phillips et al. 2004). The dimorphic niche hypothesis may explain the earlier breeding and higher success rate of smaller female snow petrels (Pagodroma nivea) compared to larger females (Barbraud & Jouventin 1998).

Here we discuss the patterns and address the potential causes of the co-occurrence of both male-biased and female-biased SSD in various morphological measurements within the Procellariiformes. Firstly we conducted a case study on SSD of the small white-faced storm petrel (Pelagodroma marina), as data on SSD in the smaller members of the Procellariiformes is
relatively scarce. Secondly, we combine these new data with a literature overview on SSD in other Procellariiformes and discuss the theories that are potentially driving the evolution and maintenance of this dimorphism within the Procellariiformes.

Methods

Study Sites

White-faced storm petrels were studied at three colonies in Victoria, Australia, between 2004 and 2008. Both Mud Islands (38°16'30"S, 144°45'00"E) and South Channel Fort are in close proximity (approximately 3km apart) within Port Phillip Bay, and Tullaberga Island (37°34'00''S, 149°51'00''E) is located more than 400kms east of Port Phillip Bay, near the border of New South Wales and Gabo Island.

Morphological Measurements

Blood samples and morphological measurements were taken from 196 breeding white-faced storm petrel adults. Adults were caught either by hand while in their burrow or in small hand nets at night when returning to the colony. Standard morphological measurements taken including: total head length (back of the head to bill tip), bill length (exposed culmen length), bill depth (immediately in front of the nostril), and tarsus length measured using plastic dial callipers (± 0.1 mm), and wing length and tail length measured using a butt-ended ruler (± 1 mm). All morphological measurements were taken by the same researcher (MU) throughout the study.

Sexing of birds

Genetic analysis was used to verify the sex of individual storm petrels. Sexing of birds was carried out by PCR amplification of the CHD gene using the primers P2 and P8 (Griffiths et al. 1998). In caught birds, blood samples (100ul to 200 mL) were collected from the brachial vein using a 26 – 29 gauge needle and a heparinised capillary tube, and stored in 70% ethanol. Liver tissue from four beach-washed white-faced storm petrels of known sex (2 males and 2 females as determined by dissection) was included as positive controls. Genomic DNA was extracted from blood and liver using the salting out method (Sunnucks and Hales 1996). PCR products were optimised using 2 μL of DNA, 1x Tag buffer (Fermentas), 2 mM MgCl₂, 200 μM of each
dNTP, 0.5 units of *Taq* polymerase (Fermentas) and 10 μm of each P2 and P8 primers in a final volume of 20 μL. The Z & W alleles, representing the two sex genes, were too similar to be separated on a 3% agarose gel. Subsequently the PCR products were digested with *Hae*III (New England Biolabs) to cut the CHD-Z PCR product into two smaller products. The digested PCR products were separated on a 3% agarose gel.

**Procellariiform Review**

Morphological measurements of Procellariiformes from 43 species across 56 populations were obtained from the literature (Appendix I). Morphological differences between the sexes were noted as either male-biased, female-biased or not significant in the particular study for measurements of total head length, bill length, bill depth, tarsus length, wing length, and tail length. These morphological measurements were chosen as they are the most commonly used measures for studies on Procellariiformes. Data on average mass of each species were obtained from del Hoyo *et al.* (1992) and Marchant and Higgins (1990). Where a range of masses was given the mean of the range was used for analysis.

**Statistical Analysis**

Data from Port Phillip Bay white-faced storm petrel populations were combined as it is known through banding records that South Channel Fort was colonised by birds dispersing from Mud Islands (Menkhorst *et al.* 1984) and less than 10 samples were obtained from South Channel Fort, hereafter referred to as Port Phillip Bay.

Statistical analysis was conducted using R, version 2.12.1 (R Development Core Team 2011). Inspection of homogeneity of variances showed little variation so therefore ANOVAs were used to investigate potential sex and geographical differences in measurements of the white-faced storm petrels. The percentage of sexual size dimorphism (SSD) between male and female means was expressed as a percentage of the male mean, where negative values indicate females are larger.

To study the potential for sex determination using biometric measurements a linear discriminant analysis was performed using the lda function in the MASS package. The jack-
knife cross validation method was used as it is the most accurate method for analysing discriminant function analysis (Dechaume-Moncharmont et al. 2011).

In the review of 56 studies of Procellariiformes (incorporating 41 species; Appendix 1) each species was categorised as being either male-biased, female-biased or having no significant difference in SSD in order to account for the variation in results provided from each study. Mann Whitney U tests were used to investigate the link between body mass and male-biased, female-biased and no difference in SSD in morphometric measurements of total head length, bill length, bill depth, tarsus length, wing length and tail length. A $p$-value of less than 0.05 was considered to be significant in all statistical tests.

**Results**

The DNA-based sexing protocol correctly identified the sex of the four beach-washed white-faced storm petrel reference individuals.

There was considerable overlap between the ranges of all morphological measurements of white-faced storm petrel males and females from both the Port Phillip Bay and Tullaberga Island populations (Figure 2.1). There was a slight geographic difference in bill depth between females from Port Phillip Bay ($n=50$) and Tullaberga Island ($F^2=5.76, p < 0.05, n=20$). Analysis of all other morphological measurements showed no significant difference in locations. There were no significant interactions between sex and location for any of the measurements. The significant result for bill depth is likely to be a result of small sample size. Thus data from both locations was combined for all further analyses.
Chapter 2 – Sexual size dimorphism

Figure 2.1 Sexual size dimorphism (SSD) of total head length, bill length, bill depth, tarsus length, wing length and tail length measurements of white-faced storm petrels (Pelagodroma marina) in Victoria, Australia. Box plots indicate median, quartiles (boxes), range (whiskers) and outliers (stars), where white boxes represent females (F), and grey boxes represent males (M). Females are significantly larger than males in their tarsus length, wing length and tail length, but smaller with respect to bill depth.
White-faced storm petrel females were significantly larger than males in tarsus, wing and tail lengths (Table 2.1). However, males had significantly larger bill depths than females (Table 2.1). All size differences were only small, the degree of SSD ranging between -2.76% to 1.70% (Table 2.1).

All morphological measurements were included in the linear discriminant analysis of the white-faced storm petrel data. The discriminant function was:

\[ D = 0.505 \text{ (total head length)} - 0.406 \text{ (bill length)} + 2.069 \text{ (bill depth)} - 0.718 \text{ (tarsus)} - 0.022 \text{ (wing)} - 0.148 \text{ (tail length)} \]

A negative score indicates a bird being female and positive score indicates a male. This correctly sexed 71% of all white-faced storm petrels (n=109, 74% of females and 68% of males; Figure 2.2). Bill depth had the largest effect on sexual size dimorphism having the highest coefficient.

In the analysis across the Procellariiformes there was a significant difference between the body mass and sex of different species for tarsus, wing and tail lengths (W = 0, \( p < 0.05 \); Figure 2.3). There is males-biased SSD in the larger species, females female-biased SSD in the smallest species, while the medium size ranged species tend to show little if any SSD (Figure 2.3). Only bill length was found not to have a significant relationship with body mass; however, this may be due to one species, Wilson’s storm petrel (Oceanites oceanicus), where bill length in females was significantly larger than that of males. In all Procellariiformes, males were always found to be significantly larger than females in total head length and bill depth measurements (Figure 2.3). For the majority of species SSD was observed in both body and bill measurements. However, there were more species (16) where only the bill was dimorphic. In the storm petrels eight species showed SSD in body size with only two species being SSD in both bill and body size.
Table 2.1 Mean (± SD) and range for morphological measurements of white-faced storm petrels (*Pelagodromonarina*) in Victoria, Australia. The percentage of sexual size dimorphism (SSD) between male and female means expressed as a percentage of the male mean (positive if males are larger and negative when females are larger).

<table>
<thead>
<tr>
<th>Measurement (mm)</th>
<th>Sex</th>
<th>n</th>
<th>Mean</th>
<th>± SD</th>
<th>Range (mm)</th>
<th>% dimorphism</th>
<th>F Value</th>
<th>p Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Head Length</td>
<td>Female</td>
<td>92</td>
<td>43.56</td>
<td>0.96</td>
<td>41.2 – 46.3</td>
<td>0.23</td>
<td>0.51</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>104</td>
<td>43.66</td>
<td>0.91</td>
<td>41.6 – 45.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bill Length</td>
<td>Female</td>
<td>71</td>
<td>17.81</td>
<td>0.49</td>
<td>16.5 – 19</td>
<td>-0.17</td>
<td>0.10</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>62</td>
<td>17.78</td>
<td>0.53</td>
<td>16.5 – 18.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bill Depth</td>
<td>Female</td>
<td>70</td>
<td>4.72</td>
<td>0.20</td>
<td>4.2 – 5.3</td>
<td>1.70</td>
<td>5.23</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>62</td>
<td>4.80</td>
<td>0.17</td>
<td>4.5 – 5.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tarsus Length</td>
<td>Female</td>
<td>91</td>
<td>43.81</td>
<td>1.06</td>
<td>40.0 – 46.2</td>
<td>-1.53</td>
<td>21.36</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>104</td>
<td>43.14</td>
<td>0.96</td>
<td>40.4 – 45.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wing Length</td>
<td>Female</td>
<td>92</td>
<td>162.47</td>
<td>4.12</td>
<td>152 – 171</td>
<td>-0.95</td>
<td>6.12</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>104</td>
<td>160.92</td>
<td>4.57</td>
<td>150 – 178</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tail Length</td>
<td>Female</td>
<td>59</td>
<td>76.71</td>
<td>2.58</td>
<td>71 – 81</td>
<td>-2.76</td>
<td>12.73</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>51</td>
<td>74.59</td>
<td>3.63</td>
<td>68 – 86</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.2 Distribution of discriminant scores of sexual size dimorphism (SSD) in white-faced storm petrel (Pelagodroma marina) males (group M) and females (group F) in Victoria, Australia. The discriminant function is:

$$D = 0.505 \text{ (total head length)} - 0.406 \text{ (bill length)} + 2.069 \text{ (bill depth)} - 0.718 \text{ (tarsus)} - 0.022 \text{ (wing)} - 0.148 \text{ (tail)}.$$  

Where a positive score indicates a male and a negative score indicates a bird being female.
Figure 2.3 Sexual size dimorphism (SSD) represented as male-biased, female-biased or no significant SSD of total head length, bill length, bill depth, tarsus length, wing length and tail length measurements against the average masses of Procellariforme species reviewed. Box plots indicate median, quartiles (boxes), range (whiskers) and outliers (stars), where white boxes represent female SSD (F), dark grey boxes represent no SSD (N), and light grey boxes represent male SSD (M). Males are always significantly larger than females in measures of total head length and bill depth. In the other measures, males exhibit larger measurements in larger species, females tend to be larger in the smallest species, while the medium size ranged species tend to show little if any SSD.
Discussion

We found that white-faced storm petrels exhibit both female-biased and male-biased SSD in their morphological measurements. Females have larger tarsus, wing and tail lengths, while males have larger bill depths. Our study is the first that has found male-biased SSD in bill depth in storm petrels, which are among the smallest representatives of the Procellariiformes. Discriminant function analysis revealed that while the differences between the sexes may be small they are significant and consequently may have ecological functions and implications. However, given the results morphological measurements alone are not a reliable tool for sexing of birds in the field. This data combined with the results of our review of the literature, the picture now emerges that when SSD exists in bill depth of Procellariiformes, males, regardless of size, have significantly larger bill depths compared to females. This review also shows that in the order of Procellariiformes SSD is related to mass for the morphological measurements of body size (tarsus, wing and tail lengths); in the larger species males-biased SSD exists, while female-biased SSD is present in the smaller species.

The seabird bill plays an important role in feeding and thus prey selection. Here we find male-biased bill depth in white-faced storm petrels and throughout the Procellariiformes. It is likely that any selection for evolution of SSD to reduce intra-specific competition for food or foraging, associated with the ecological hypothesis, is most likely to affect the bill morphology (Selander 1966, Nebel & Thompson 2011). Differences in foraging locations and diets of some species have been recorded and this may be related to SSD (Shaffer et al. 2001; Copello et al. 2006). Bill measurements have been found to be the most dimorphic of all the measurements of many Procellariiformes (Copello et al. 2006; Bull et al. 2005; Burgoni & Furness 2009; Eionder et al. 2008). We found no relationship between bill measurements and body mass of the species studied; however bill depth was consistently larger in males in the majority of species. In addition more species exhibit SSD in bill measurements compared to those measures of body size.

The dimorphic niche hypothesis has been used in birds to correlate female size and clutch size (Hedrick & Temeles 1989). As with many seabirds, all Procellariiformes lay only a single egg. This reduced clutch size is thought to be a result of the high energetic costs of foraging on distant resources (Lack 1968). Although Procellariiformes only lay a single egg the size of their
egg is the largest in relation to their body weight in any bird species (Rahn 1975). We found that reversed SSD occurs in the smaller Procellariiformes, such as the storm petrels, which lay the largest eggs of all, in proportion to the body mass, being over 25% of adult body mass (Croxall 1984; 1995). Storm petrels seldom have a guard stage once the chick has hatched and as such the chicks need to be well developed soon after hatching (Warham 1990). Therefore the dimorphic niche hypothesis, and thus egg size may be the driving force behind this reverse SSD with decreasing size in Procellariiformes.

Interestingly, these patterns of SSD observed in adult white-faced storm petrels were also found to follow a similar trend in chicks prior to fledging (Chapter 3). This could be the result of developmental constraints but it is possible that the SSD observed in white-faced storm petrels may play an important role in the ecology of the species from very early on and could be related to the dietary segregation during migration and in the wintering grounds (Chapter 6).

Lack (1968, p.161) stated that “Some size differences have evolved in relation to sexual behaviour and others for ecological reasons”. Within the order of Procellariiformes we find an excellent example of this contention; the direction of sexual size dimorphism in Procellariiformes’ body size changes from male-biased to female-biased in the smaller species, whilst bill dimorphism, the most dimorphic measurement in the majority of species of Procellariiformes, remains male-biased. It thus appears that two different ecological processes are influencing the SSD observed in Procellariiformes. Firstly, large egg size, relative to body size, may be driving reversed SSD in smaller Procellariiformes. Secondly, differences in foraging and diet may in fact be influencing the selection of bill size in all Procellariiformes. Although the degree of SSD observed in some species may be minute, these differences may still play an important ecological role.
References


### Appendix 1: Sexual size dimorphism (SSD) in the Procellariiformes

Where SD = sexual dimorphism, THL = total head length, BL = bill length (Culmen Length), BD = bill depth, TL = tarsus length, WL = wing length, Tail = tail length. Within the table the direction of significant SSD is indicated by M = males, F = females and N = not significant. A dash indicates that the particular measure was not included in that study. Mass data was obtained from del Hoyo et al. (1992) and Marchant & Higgins (1990).

<table>
<thead>
<tr>
<th>Species</th>
<th>SD</th>
<th>Mass (g)</th>
<th>THL</th>
<th>BL</th>
<th>BD</th>
<th>TL</th>
<th>WL</th>
<th>Tail</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macronectes giganteus</td>
<td>Y</td>
<td>4400*</td>
<td>-</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>N</td>
<td>Bugoni &amp; Furness (2009)</td>
</tr>
<tr>
<td>Macronectes giganteus</td>
<td>Y</td>
<td>4400*</td>
<td>-</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>-</td>
<td>Copello et al. (2006)</td>
</tr>
<tr>
<td>Diomedea melanophris</td>
<td>Y</td>
<td>4000*</td>
<td>-</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>M</td>
<td>M</td>
<td>Bugoni &amp; Furness (2009)</td>
</tr>
<tr>
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<td>Y</td>
<td>3900*</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>N</td>
<td>N</td>
<td>Hedd et al. (1998)</td>
</tr>
<tr>
<td>Diomedea chlorhydra</td>
<td>Y</td>
<td>2710*</td>
<td>-</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>N</td>
<td>M</td>
<td>Bugoni &amp; Furness (2009)</td>
</tr>
<tr>
<td>Procellaria aequinoctialis</td>
<td>Y</td>
<td>1220*</td>
<td>-</td>
<td>M</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Bugoni &amp; Furness (2009)</td>
</tr>
<tr>
<td>Puffinus gravis</td>
<td>Y</td>
<td>833*</td>
<td>-</td>
<td>N</td>
<td>M</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Bugoni &amp; Furness (2009)</td>
</tr>
<tr>
<td>Puffinus gravis</td>
<td>Y</td>
<td>833*</td>
<td>-</td>
<td>N</td>
<td>M</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Bull et al. (2005)</td>
</tr>
<tr>
<td>Puffinus gilletti</td>
<td>N</td>
<td>814*</td>
<td>-</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Bull et al. (2005)</td>
</tr>
<tr>
<td>Fulmarus glacialis</td>
<td>Y</td>
<td>800*</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>N</td>
<td>van Franeker &amp; Ter Braak (1993)</td>
</tr>
<tr>
<td>Fulmarus glacialoides</td>
<td>Y</td>
<td>800*</td>
<td>-</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>N</td>
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<tr>
<td>Fulmarus glacialoides</td>
<td>Y</td>
<td>768*</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>van Franeker &amp; Ter Braak (1993)</td>
</tr>
<tr>
<td>Species</td>
<td>SD</td>
<td>Mass (g)</td>
<td>THL</td>
<td>BL</td>
<td>BD</td>
<td>TL</td>
<td>WL</td>
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Chapter 3

**Does small sexual size dimorphism influence chick size, growth rates, provisioning rates and meal size? – A case study of the white-faced storm petrel**

(*Pelagodroma marina*)
Abstract

Differences in the sexual size dimorphism (SSD) of a species can result in increases in energetic costs to parents to produce a particular sex. Ultimately, a trade-off between adult condition and breeding success may result in a bias in offspring sex, potentially having long-term implications on a population. The white-faced storm petrel (Pelagodroma marina) exhibits SSD in both directions with regards to different aspects of their morphology. We found that white-faced storm petrels chicks exhibit similar patterns of SSD to adults prior to fledging. However, we found no difference in growth rates, meal sizes or provisioning rates of white-faced storm petrel chicks, which suggests that there is no extra energetic costs to adults in raising either sex. SSD observed in white-faced storm petrel chicks may be a potentially important aspect of their post-fledging ecology.

Introduction

Sexual size dimorphism (SSD) in offspring can present an increased energetic cost to the adults due to higher provisioning costs of the larger sex (Clutton-Brock 1991, Daunt et al. 2001, Cameron-MacMillan et al. 2006). For example, in the case of the brown songlark (Cinclorhamphus crualis) male chicks are 49% larger than female chicks at 10 days of age. In manipulated, single-sex broods, female adults delivered 43% more prey items and expended 27% more energy when provisioning all male broods compared to all female broods (Magrath et al. 2007). In addition, adult survival and subsequent breeding attempts can be affected by raising a particular sex (Clutton-Brock 1991). Consequently, in the case of sexual size dimorphism in offspring, opting for raising the larger or smaller sex is probably an important trade-off between the condition of parent birds and the fitness expectations of male and female offspring (Trivers & Willard 1973, Clutton-Brock 1991).

Differences in required parental investment between chicks of different sex might potentially result in undesirable sex-ratio changes in animal populations under environmental stress, where parents may opt for the “cheaper sex” when conditions become unfavourable. It is likely that offspring sex (ratio) may be manipulated to at least some extent (Trivers & Willard 1973). Given the population decline of white-faced storm petrels (Pelagodroma marina) and the
concomitant concerns regarding their conservation status (Menkhorst et al. 1984), investigating potential differences in the energy requirement of the sexes warrants investigation.

The white-faced storm petrel is a small Procelariiform which lays only a single egg and has extended incubation and chick rearing periods, as found in all Procellariiformes (Warham 1990). Reversed sexual size dimorphism occurs in adult white-faced storm petrels with females being 0.95 – 2.76% larger in overall structural measurements such as tarsus and wing length; however, males still have significantly larger bill depths (1.70 %) than females. Whether this same pattern applies to chicks is unknown. If SSD occurs in white-faced storm petrel chicks then we would expect that females being larger would obtain higher peak weight and have higher growth rates compared to males. Here we investigate if the sexual size dimorphism apparent in adult white-faced storm petrels is also reflected in chick growth rates, provisioning rates and meal sizes. Further we discuss the potential consequences this dimorphism may have for the parent birds.

Methods

This study was undertaken at Mud Islands, Port Phillip Bay, Victoria (38°16’30”S, 144°45’00”E), during the 2005/06 and 2006/07 breeding seasons. Study burrows were monitored between December and March to determine feeding frequency, meal sizes and growth rates of chicks. Access to chicks was obtained via a short access tunnel dug directly in front of the nesting chamber and was covered with a small wooden board to prevent damage to the burrow from frequent access. In order to determine more accurately chick hatching dates, burrows were checked almost daily during this period. Where hatching dates were unknown, chick age was estimated based on mass and morphological measurements of known age chicks and hatching dates inferred.

Chick Growth

Growth rates of chicks (from 18 and 30 burrows during the 2005/06 and 2006/07 breeding seasons, respectively) were determined by weighing (using an electronic scale to 0.1 g) and recording of measurements of total head length, bill length, bill depth, tarsus length (with dial callipers ±0.1 mm) and wing length (using a butt ended ruler ±1.0 mm) throughout the
nestling period at 2 – 10 day intervals. Blood samples were taken for sex determination of chicks (following chapter 2). A Gompertz growth equation was fitted to body mass measurements of males and females separately following Ricklefs (1968):

\[ M = A e^{b \cdot e^{-Kt}} \]

where \( M \) is body mass (g), \( A \) is asymptotic body mass (g), \( b \) is the time constant (d), \( K \) is the growth constant (d\(^{-1}\)) and \( t \) is chick age (d). Gompertz equations have previously been found to be the ‘best fit’ for chick growth in Procellariiformes (Hedd et al. 2002). Only chick mass up to an age of 50 days were included in the equations as after this point their mass declines prior to fledging.

**Meal Sizes**

Feeding frequency and meal sizes of 28 chicks were recorded by repeated weighing at 4-hour intervals (using an electronic scale to 0.1 g) throughout the night for 20 nights during the 2006/07 chick rearing period. These weighings took place at 20:00, 24:00, 04:00, and 08:00, as adult storm petrels only return to the colony well after dark and depart before first light. Each set of weighings took approximately one hour to complete and chicks were always weighed in the same order. No chicks regurgitated any food while being weighed. The increase in mass alone does not accurately reflect the true size of the meal delivered to the chick due to mass loss through respiration and regular excretion. In order to account for this and record the actual size of the meals received by the chick we adopted the procedure developed by Ricklefs *et al.* (1985) using

\[ e_m = -t(l_1 + l_2)/2 \]

Where \( e_m \) is the bias in meal size (g), \( t \) is time between weighing (h), \( l_1 \) the rate of mass loss in the 4 hours prior to receiving a meal and \( l_2 \) the rate of mass loss in the 4 hours following a meal (g/h). Both \( l_1 \) and \( l_2 \) were estimated over periods of 4 hours (\( t \)) in which no meal was apparently being fed and that were respectively preceding and following a period in which a meal was being fed. Due to differences in metabolic rates of chicks at different ages, we based the values in the equation for all chicks in 10 day age classes. The adjusted meal size value was used for all meal size analyses.

A meal was defined as the total increase in the mass of the chick between 20:00 and 8:00. A chick was considered to have received two feeds if there were 2 independent increases in mass.
over two separate time periods without an adult being present in the burrow at the time of weighing or alternatively when both adults were seen in the burrow during the night.

**Statistics**

Statistical analysis was conducted using R, version 2.12.1 (R Development Core Team 2011). Nonlinear regression analysis of chick mass over the chick rearing period was used to determine parameters for the Gompertz equation of chick growth. Generalised linear models of meal size were undertaken using the lme function from the nlme library, where individual was a random factor to account for multiple measurements from the same individuals. Morphometric data were analysed using ANOVA to determine any differences between the sexes. A *p*-value of less than 0.05 was considered to be significant in all statistical tests.

**Results**

**Sexual Size Dimorphism**

There was considerable sexual size dimorphism in chicks prior to fledging (age >50 days), resembling the patterns seen in adults (Figure 3.1). Females have larger tarsus length (*F*=5.83, *p*=0.02, one-sided) and showing tendencies for larger wing lengths (*F*=3.93, *p*=0.056, one-sided) and tail lengths (*F*=0.83, *p*=0.37, one-sided) compared to males (Figure 3.1). However, male chicks had slightly larger bill depths than females (*F*=0.47, *p*=0.50, one-sided).

**Chick Growth**

The mass of white-faced storm petrel chicks followed a pattern typical for all Procellariiformes with a relatively rapid initial growth to an asymptotic level in excess of adult mass (around 50g), after which body mass declined prior to chick fledging (Figure 3.2). Gompertz growth curves were fitted to body mass measurements of both male and female chicks up to an age of 50 days. There was considerable overlap in all Gompertz equation parameter estimates for both males and females, suggesting that the growth rate of chicks is similar for both sexes (Table 3.1; Figure 3.2).
Figure 3.1 Sexual size dimorphism (SSD) of total head length, bill length, bill depth, tarsus length, wing length and tail length measurements of white-faced storm petrels chicks (*Pelagodroma marina*) in Victoria, Australia. Box plots indicate median, quartiles (boxes), range (whiskers) and outliers (stars), where white boxes represent females (F), and grey boxes represent males (M). Arrows represent approximate median values from adult white-faced storm petrels for each measurement (from chapter 2).
Table 3.1 Parameter estimates (± 95% CI of the mean) for Gompertz growth curves fitted to body mass measurements of male and female white-faced storm petrel (*Pelagodroma marina*) chicks in Victoria, Australia. $A$ is asymptotic body mass (g), $b$ is the time constant (d), $K$ is the growth constant (d$^{-1}$).

<table>
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<td>68</td>
<td>64 – 73</td>
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<td></td>
<td>♂</td>
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<td>61 – 69</td>
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<td>$b$</td>
<td>♀</td>
<td>1.78</td>
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<td></td>
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<td>$K$</td>
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<td>0.082</td>
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<td>0.089</td>
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**Meal Size**

We recorded 367 meal feeds during the study. Chicks were fed on 70% of nights ($n$=620 chick nights). Male chicks were fed on 72% of nights while females were fed on 67% of nights. The longest period of time a chick went without being fed was 3 days, while chicks were also found to be fed on at least 6 consecutive nights. Some chicks were still found to be fed close to fledging age.

To provide a more accurate estimate of meal size the equation values for $I_1$ ranged from 0.5 – 1.9 g and values for $I_2$ ranged from 1.5 – 3.0 g across all 10 day age categories (following Ricklefs et al. 1985). Consequently the values for the correction to meal size ranged from 3.9 g for the 1-10 day old chicks and the highest adjustment value of 9.7 g for chicks aged 41 – 50 days. The adjusted size of meals averaged 17.6 g (range 5.6g to 35.2g). Mean meal size for female chicks was 13.3 g (± 5.0 SD, range 5.1 – 25.8, $n$=199) and for males 12.5 g (± 5.94 SD, range 3.7 – 35.2, $n$=168). Chicks were found to receive two feeds in a single night on at least 35 occasions.
Figure 3.2 Body mass (upper panel) and meal size (lower panel) as a function of age, where chick masses follow a similar pattern to meal size in both male and female white-faced storm petrels (*Pelagodroma marina*) chicks. Body mass: mean ± SE (g) per 5 day age classes; meal size: median, quartiles (boxes), range (whiskers) and outliers (circles) (g) per 10 day age classes; white boxes represent females (squares), and grey boxes represent males (triangles).
Where chicks received two meals on a single night the size order of the meals was found to vary. With thirteen chicks receiving a large meal followed by a smaller meal, 11 receiving a small meal followed by a larger meal, and 7 approximately equal sized meals. There were some nights where both adults were seen in the burrow, sometimes concurrently, yet the chick received only a very small meal. It may also be possible that non-feeding visits by adults occur.

Prior to reaching peak body mass, meal size was found to be positively correlated with chick age, meal sizes decreasing thereafter (Figure 3.2). Generalised linear models were run with meal size as the dependent variable and combinations of sex, age (in d as covariate), age\(^2\) and their interactions as explanatory variables. None of the interaction terms were found to be significant and were removed from the model. There were significant differences in meal size for both age and age\(^2\) (t= 3.35 & -3.73 respectively, \(p<0.05\), \(n=207(24\) individuals)). No significant differences in meal size between the sexes were found.

**Discussion**

Despite white-faced storm petrel chicks still being structurally smaller than the adults prior to fledging, they appear to express some sexual size dimorphism at this early age. This pattern is very similar to that observed in adult white-faced storm petrels with females generally larger in structural measurements such as tarsus and wing length, whilst males tend to have larger bill depths (Chapter 2).

Procellariiform chick growth begins slowly then increases rapidly until reaching a plateau after which body mass decreases slightly prior to fledging (Warham 1990). This pattern was also observed in this study of white-faced storm petrel chicks. Given the differences in SSD of white-faced storm petrel chicks we would expect the larger sex, the female chicks, to have a quicker growth rate and to obtain a higher maximum weight compared to males. Studies of shy albatross (*Thalassarche antarctica*) have shown that males (being the larger sex in this case) grew faster, attained higher weight and received more food than the female chicks (Hedd et al. 2002). However, in this study we found no differences in any of these attributes between male and female white-faced storm petrel chicks. As with other Procellariiformes, the white-faced storm
petrel chicks exceeded the weight of the adults at their peak weight. This strategy of having ‘obese’ chicks consequently allows them to survive longer periods without being fed, allowing adults to undertake longer foraging trips. Thus the similar growth rate exhibited by male and female white-faced storm petrel chicks may be a consequence of foraging strategies undertaken by adults in order to take advantage of distant foraging areas and fluctuations in food availability.

This study found that meal size followed a similar pattern as chick growth and was strongly influenced by the age of the chick, increasing with chick growth before declining prior to the chick fledging. Meal size also varied considerably; however, we found no difference in the size of the meals fed to white-faced storm petrel chicks. Previous studies found that if thin-billed prion (Pachyptila belcheri) chicks are in poor condition the adults generally respond by providing larger meals (Quillfeldt et al. 2006). Similarly in shy albatross, both adults provision equally and are able to alter provisioning rates in response to chick needs (Hedd et al. 2002). Thus adult Procellariiformes appear to be able to adjust provisioning and feeding based on the condition and growth requirements of the chick suggesting that these factors are likely to have a greater influence on provisioning rates compared to differences in chick sex.

Both growth and provisioning rates of white-faced storm petrel chicks are similar between the sexes suggesting that there are no extra energetic costs to parents associated with raising a chick of either sex. However, SSD is still exhibited in white-faced storm petrel chicks prior to fledging and may be relevant for other aspects of their ecology, such as diet and foraging behaviour, post-fledging.
References


Chapter 4

THE EFFECT OF SEXUAL SIZE DIMORPHISM ON FORAGING BEHAVIOUR IN PROCELLARIIFORMES
Abstract

Sex differences in foraging behaviour and parental investment have been found in both monomorphic and dimorphic seabirds. These differences may be related to differences in size of a particular sex. In Procellariiformes sexual size dimorphism (SSD) occurs in both directions with some species being monomorphic. Here we studied the incubation and foraging behaviour of a small Procellariiform, the white-faced storm petrel (*Pelagodroma marina*), which exhibits minor reversed SSD. Differences in incubation shift and foraging trip duration were found between male and female white-faced storm petrels and breeding season. During chick rearing, females spend a greater proportion of time on long foraging trips compared with males who spend a greater proportion of time on short foraging trips. These differences in foraging behaviour suggest there may be potential inter-sexual segregation of foraging areas for white-faced storm petrels. This may be a result of subtle SSD in bill morphology which can influence diet and prey selection and consequently potential foraging distributions.

Introduction

Seabirds have developed various life history traits and strategies to cope with the unpredictability and patchiness of the marine environment (Lack 1968, Warham 1990). Procellariiformes (albatrosses and petrels) have developed additional strategies to cope with these environments including: egg neglect, where an egg can be left unattended for short periods of time while remaining viable (Pefaur 1974, Boersma et al. 1979); converting food into energy dense stomach oil following long foraging trips (Obst *et al.* 1987); overfeeding chicks to develop fat stores to cope with long periods without being fed (Lack 1968); and a dual foraging strategy with alternating short and long foraging trips (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1994). In addition, Procellariiformes are generally long-lived species that lay a single egg and have extended incubation and chick rearing periods (Lack 1968). All of these strategies assist Procellariiformes to exploit more productive foraging areas further away from the breeding colony (Lack 1968, Warham 1990).

Bi-parental care occurs in 81% of all bird species, including the Procellariiformes (Cockburn 2006). However, the contribution to parental care can be biased towards a particular sex.
Chapter 4 – Foraging behaviour

(Trivers 1972). These differences can result from differences in foraging behaviour and dimorphism of a species. Sexual size dimorphism (SSD) occurs in many species of Procellariiformes and can be either male or female-biased (Chapter 2). These differences in dimorphism can influence an individual’s ability to contribute to the reproductive effort.

There are two hypotheses proposed surrounding SSD in relation to foraging behaviour and parental investment. Firstly, the dimorphic niche hypothesis suggests that sexual size dimorphism within a species can arise due to differences in their reproductive roles and/or differences in parental investment (Fairbairn 1997), which may explain the bias observed in some species. Secondly, variation in foraging strategies between the sexes may be a result of ecological niche segregation, a hypothesis that proposes that differences in the foraging areas of males and females reduce inter-sexual competition (Fairbairn 1997). In the majority of Procellariiformes where the male is the bigger more dominant sex, males undertake shorter foraging trips compared to females, which is believed to result from males dominating the foraging areas close to the colony driving the smaller sex further afield to forage (González-Solis 2000).

This study investigates the nest attendance and foraging strategies employed by the white-faced storm petrel (*Pelagodroma marina*) breeding at Mud Islands, Victoria, Australia (38°16′30″S, 144°45′00″E). The white-faced storm petrel shows reversed SSD where females are slightly larger than males in most body measurements, except for males having larger bill depths (Chapter 2). While size differences are only subtle they may still influence the contribution of each sex to the reproductive effort and/or foraging behaviour. This population is unique in that they breed within an embayment compared to other colonies which are generally offshore, and consequently may need to travel further to reach productive offshore feeding grounds. Given females in the white-faced storm petrels are larger, we would expect females to exhibit more frequent and shorter foraging trips compared to males as is found in giant petrels (González-Solis 2000). However, this may be confounded by the males having larger bills, which may influence diet and prey selection (Chapter 5), in turn affecting foraging behaviour. Here, we examine the relationship between incubation and foraging behaviour, and breeding success of white-faced storm petrels at Mud Islands, Victoria, during two consecutive breeding seasons. Given the subtle SSD in this species in contrast to previous studies within this order,
we hope it will shed more light on the standing hypotheses on the role of SSD on parental care in Procellariiformes.

Methods

We studied the nest attendance and foraging trip duration of breeding adults of the white-faced storm petrel during the austral summer of 2006/2007 and 2007/2008. The breeding season begins when birds arrive at the colony from August with eggs laid from late October and incubated for approximately 50 days. Chicks hatch in December and the majority fledge by late February to mid-March (Underwood and Bunce 2004).

Breeding Biology

During the breeding period of the austral summer of 2006/07 and 2007/08 a total of 57 and 29 white-faced storm petrel burrows were monitored, respectively. Access to adults was obtained via a short access tunnel dug directly in front of the nesting chamber and then covered with a small wooden board. Study burrows were checked approximately weekly prior to egg-laying and throughout the breeding period until the chicks had fledged. Control burrows were checked less frequently to ensure that there was no investigator disturbance. Breeding success was defined as a pair raising a chick to fledging age.

Foraging Trip Duration

In each season, a subset of 18 and 12 burrows, respectively, were selected within the study site to investigate the nest attendance and foraging trip duration of adult white-faced storm petrels during the breeding period. All burrows were located within a 5m radius. A small TIRIS transponder (Texas Instruments Registration and Identification System) weighing 0.6 g was attached to the two central tail feathers of parent birds using Tesa tape and a small amount of Loctite ® 401 glue. A circular antenna was placed at the burrow entrance and was connected to an Amskan recorder powered by a small solar powered battery. The antenna has a range of approximately 10-15 cm in which it can detect the presence of a transponder. The recorder was set on the fastest constant recording speed where a reading is taken from each antenna every 1.5 s to detect the presence of a transponder. As a bird passed over the antenna when it enters or departs a burrow the unique identification number, date, time and antenna number...
were logged. The 1.5 s interval allowed sufficient time for the natural movement of the bird into the burrow (cf. Zangmeister et al. 2009 using 30 s intervals for their study of Leach’s storm petrel, *Oceanodroma leucorhoa*). In this study, the recorder was set to only log the tag number once every 5 seconds to avoid an excessive number of records. In most cases the tag number was recorded multiple times for each entry and departure from the burrow and we are therefore confident that all arrivals and departures to and from the nest were recorded. White-faced storm petrels do not return to the burrow until well after dark and leave before first light. The Amskan recorder was therefore set to record between 7pm and 7am daily to conserve battery power.

Where possible both adults from each burrow had a TIRIS tag attached. All birds were banded with metal alloy bands supplied by the Australian Bird and Bat Banding Study (ABBBS). Blood samples from at least one partner in each study burrow were taken for molecular based sex determination from which the sex of both parents was inferred. A small blood sample (less than 1 mL) was taken from a small puncture to the brachial vein and stored in 70% ethanol (following chapter 2).

During the first season (2006/07) the system was installed part-way through the incubation period. In the second season (2007/08) it was installed at the beginning of the incubation period. Due to technical problems one Amskan reader failed to record any data between the 15th December 2006 and 16th January 2007. In addition, some birds lost their TIRIS tag after only a few trips, because the feathers were either falling out or breaking off. Where possible the antenna was moved to another nearby burrow and a tag attached to each individual of a new pair. In addition, if neither adult had been recorded in the burrow for a number of days it was deemed to be unsuccessful and the antenna was moved to a nearby burrow.

Foraging trip data was separated into two periods; i) the incubation phase, which included nest attendance immediately prior to, during hatching, as well as the immediately following brooding of the hatchling, and ii) the chick rearing phase, from when the chick was first left alone in the burrow during the day, until the chick had reached fledging age and was no longer seen in the burrow. Data collected during the incubation period was analysed separately from data collected during the chick rearing period. During the chick rearing phase some birds had
multiple short visits to their burrow in a single night at 10-15 minute intervals. We assumed that adults did not forage during these short intervals, and therefore only the first and last recorded visit were considered.

**Statistical Analysis**

Statistical analysis was undertaken using the R package 2.15.0 (R Development Core Team 2011). Chi-square tests were used to analyse breeding success of study and control burrows. All nest attendance and foraging trip durations were analysed using generalised linear mixed models (GLMM) with a Poisson distribution. Alternatively, given the fact that no shifts took place during the daylight hours, incubation shifts and foraging trips were treated as whole days (ie. 1 day, 2 day etc.). Foraging trip duration was also categorised as either short trip (1 – 2 days) or long trip (3+ days; following Baduini & Hyrenbach 2003). For these analyses GLMM with a binomial distribution were used. Incubation and chick rearing periods were analysed separately. Models included adult sex, breeding success (where success was defined as chick fledged), breeding season, and chick age class (10 day age classes) and chick sex as factors. The individual tag identification number was treated as a random effect to control for multiple records from the same individuals. Wilcoxon non-parametric tests were also used to determine differences in incubation shifts and foraging trips between the sexes. A \( p \)-value < 0.05 was considered to be significant.

**Results**

The overall breeding success in the colony was 52% during the first breeding season and 30% during the second season. There was no significant difference in success between study burrows and control burrows within the colony in either season (\( \chi^2=0.67, p=0.42 \)).

**Incubation Period**

Incubation shifts ranged from 5 hours to 7 days during the incubation period (\( n=105 \)). Adult males had significantly shorter incubation shifts than females (\( W=1583, p=<0.05; \) Figure 4.1). Male mean incubation shift was 2.38 days (\( \pm 0.225 \) SE, median=2.05, \( n=69 \)), and for the females it was 3.33 days (\( \pm 0.315 \) SE, median=3.15, \( n=36 \)). Seven individuals spent less than 5 hours in the burrow during the incubation period (total of 18 trips). The model including both
factors and their interactions (sex, season, success) found male incubation shifts were significantly shorter than that of females ($z = -2.241, p < 0.05$). In addition, the interaction sex × breeding success showed that males that successfully raised a chick to fledging had significantly longer incubation shifts ($z = 1.897, p < 0.05$). When each factor was modelled individually, breeding success was the only factor to be significant, with incubation shifts longer in those nests that were ultimately successful ($z = 2.796, p < 0.05$). The AIC value of this model was also slightly higher than the full model (AIC 161.9 compared to 156).

Foraging trip duration ranged from 1-8 days during the incubation period ($n = 116$). The mean male foraging trip was 2.59 days ($\pm 0.211$ SE, median=1.96, $n = 75$); significantly shorter than the mean female foraging trip, 3.48 days ($\pm 0.335$ SE, median= 3.88, $n = 41$; $W = 1928, p < 0.05$; Figure 4.1). Males spend nearly twice as much time undertaking single day foraging trips compared to females (Figure 4.1).

**Chick Rearing Period**

The mean foraging trip during the chick rearing period was 1.89 days (0.09 $\pm$ S.E., $n = 237$), typically ranging from 1-7 days, with a single 9 day trip recorded (Figure 4.2). There was no significant difference in the male and female mean foraging trip duration ($W = 5424, p > 0.05$); mean male foraging trip was 1.77 days ($\pm 0.102$ SE, median=1.05, $n = 75$), while for females it was 2.10 days ($\pm 0.174$ SE, median= 1.00, $n = 41$).

Single day foraging trips represented 56% of all trips in both male and female white-faced storm petrels. One individual male was found to continue returning to the nest 5 times over a week following the chick’s fledging. Males spent the majority (76%) of the chick-rearing period undertaking short foraging trips with infrequent longer trips. In contrast, females spent only 63% on short trips and spent a greater proportion of their time on long trips compared to males (Figure 4.2). When foraging trip duration was categorised as either a short and long trip, the models for individual factors found a significant difference between the sexes with males making more short trips than females ($z = 2.094, p < 0.05$). Also there were significant differences seasonally, with the second season (2007/08) having slightly shorter trips ($z = 2.114, p < 0.05$).
Figure 4.1 Frequency distribution of incubation shift and foraging trip duration of male (grey bars) and female (white bars) white-faced storm petrels (*Pterodroma marina*) at Mud Islands, Victoria, during the incubation period in the 06/07 and 07/08 breeding seasons.
Figure 4.2 Frequency distribution of foraging trip duration of male (grey bars) and female (white bars) white-faced storm petrels (*Pelagodroma marina*) at Mud Islands, Victoria during chick rearing in the 06/07 and 07/08 breeding periods.
Discussion

This study shows differences in the incubation and foraging behaviour of male and female white-faced storm petrels. Males undertake a greater proportion of short foraging trips throughout the breeding period, whereas females tended to undertake a greater proportion of long foraging trips. Differences in incubation and foraging trip durations varied between seasons. In addition, breeding success also varied with incubation and foraging behaviour of adult white-faced storm petrels.

Incubation period

Generally, during the incubation period female Procellariiformes are in poorer condition as they have expended considerable energy in egg production & laying (Warham 1990). Therefore, during the incubation period, females are more likely to undertake extended foraging trips in order to recuperate and improve their individual condition (Weimerskirch et al. 1994, Weimerskirch et al. 1997, Ochi et al. 2010). Consistent with this notion, this study found that female white-faced storm petrels also have significantly longer incubation shifts and foraging trips than males. The high proportion of short trips made by male storm petrels during the incubation period suggests that they are returning to the burrow frequently for shorter incubation shifts. Similar differences in attendance patterns of the sexes have been observed in Leach’s storm petrel and the streaked shearwater (Calonectris leucomelas; Mauck et al. 2011, Yamamoto et al. 2011).

Nevertheless, this study found shorter foraging trip durations by white-faced storm petrels are more likely to result in unsuccessful breeding attempt. Zangmeister et al. (2009) found a similar pattern in Leach’s storm petrel. There appears to be trade-off between more frequent shorter foraging trips and longer incubation for males if they are to successfully fledge a chick.

Chick Rearing

The white-faced storm petrel has a considerably greater variation in foraging trip durations (1 – 9 days) compared to other storm petrel species such as the European storm petrel (Hydrobates pelagicus), 1-2 days, and Leach’s storm petrel, 1-4 days (Badunini & Hyrenback 2003). The white-faced storm petrel in Victoria also has a more synchronised breeding season, approximately 2 ½ months shorter than the similar sized European white-faced storm petrel.
subspecies *Pelagodroma dulcia hypoleuca* (Underwood & Bunce 2004, Campos & Granadeiro 1999). In addition, the maximum weight of the white-faced storm petrel chick varies between the Victorian and European subspecies, with the former attaining a higher maximum weight (Underwood & Bunce 2004, Campos & Granadeiro 1999). All these differences may be due to geographical differences in the proximity of foraging resources to breeding colonies, rather than any specific phylogenetic differences among the species. These variations may be driven by seasonal availability of prey. Alternatively, they may also be due to differences in migration with the southern hemisphere species (including juveniles) undertaking trans-equatorial migration north, whereas northern hemisphere species do not undertake major migrations but rather disperse from their breeding colonies (Warham 1990).

During chick rearing the white-faced storm petrels spent approximately half their time undertaking short 1-2 day foraging trips while the remainder of trips were longer durations. This pattern of foraging has also been reported in wandering albatross (*Diomedeas exulans*, Weimerskirch *et al.* 1997), manx shearwater (*Puffinus puffinus*, Gray & Hamer 2001), and wedge-tailed shearwater (*Puffinus pacificus*, Peck & Congdon 2006). A dual foraging strategy, where individuals alternate short and long trips, has been reported in a number of Procellariiformes (see review: Baduni & Hyrenbach 2003). It has been suggested that a dual foraging strategy allows seabirds to take advantage of more distant food resources, allowing them to forage more efficiently (Weimerskirch *et al.* 1997). While this strategy has not previously been shown to occur in storm petrels, it is possible that due to the white-faced storm petrels from Mud Islands being close to land and a great distance from the productive foraging areas, they may indeed employ this dual foraging strategy in order to take advantage of the more distant resources.

Little is known of the at-sea distribution of white-faced storm petrels. There was a trend for females to undertake a higher proportion of longer foraging trips compared to males. While during the incubation period this also influenced by the success of the nest, during the chick rearing period all individuals monitored reared a chick successfully to fledging. Additionally, 20% of foraging trips made by male white-faced storm petrels were short, two-day trips, while females made few short foraging trips. These differences in the proportion of short and long trips between male and females may also suggest that the sexes are foraging in different
locations. While the diet of white-faced storm petrels revealed little variation in prey species between the sexes, they appear to target different size classes of some prey species (Chapter 5). The variation in foraging strategies of male and female storm petrels observed here could be a means of reducing intersexual competition in foraging areas.

**Parental investment and SSD in Procellariiformes**

Procellariiformes exhibit varying degrees of sexual size dimorphism and can be male-biased or female-biased. Despite these differences in direction and degrees of SSD it appears that generally females undertake a greater proportion of long foraging trips, whilst males make a greater proportion of shorter trips. This is in contrast to the expected findings with male white-faced storm petrels, being the smaller sex, expected to have longer trip durations. It would appear that body size has little effect on foraging behaviour in Procellariiformes. Thus, differences in bill morphology that are thought to influence diet and prey selection may influence the foraging distributions of the white-faced storm petrel based on food availability.
Chapter 4 – Foraging behaviour

References


Chapter 5

INTERSEXUAL DIFFERENCES IN PREY SELECTION IN THE NEAR-MONOMORPHIC WHITE-FACED STORM PETREL (*Pelagodroma marina*)
Abstract

Morphological attributes can directly influence the type and size of prey available to and selected by seabirds. Consequently, even subtle differences in morphology have the potential to cause variation in diet. In sexually dimorphic species with subtle differences in bill morphology, this may lead to diet and niche segregation. The white-faced storm petrel (*Pelagodroma marina*) exhibits a small degree of sexual size dimorphism in bill morphology where males have slightly larger bills than females. Here we studied the diet of white-faced storm petrels in two colonies in Victoria, Australia, over two consecutive breeding seasons. Crustaceans and fish represented a high proportion of the white-faced storm petrel diet. Of recognisable prey remains, at least 25 taxa were identified, with coastal krill (*Nyctiphanes australis*) being the most abundant overall (25.7% numerical abundance). Differences in diet were found between locations and between seasons suggesting that storm petrels are opportunistic feeders and able to adapt their diets when necessary. While there were no overall significant differences in prey-species composition between the sexes, prey size targeted by males and females varied significantly and may be a consequence of differences in sexual size dimorphism (SSD).

Introduction

Differences in morphology, both between and within seabird species, can result in variation of diet and segregation of foraging areas (Selander 1966, Ashmole & Ashmole 1967). The inter-sexual niche divergence hypothesis (or ecological sexual dimorphism hypothesis; Fairbairn 1997) suggests that intersexual differences in morphology may evolve to reduce inter-specific competition for resources. The Procellariiformes (albatrosses, petrels and shearwaters) exhibit sexual size dimorphism (SSD) in both directions, with males being larger in the larger species, such as albatross and giant petrels, and females being larger in the smaller species, such as storm petrels (Chapter 2). The degree of dimorphism also varies along this size gradient with larger species having larger differences between the sexes, whereas the differences between the smaller species are much more subtle (Rensch 1966). The drivers of the evolution and maintenance of SSD in Procellariiformes appear to be influenced by ecological processes relating to reproduction and foraging ecology (Chapter 2).
Besides feeding, the seabird bill has a wide range of additional uses and functions, including territory defence during breeding and mate attraction (Warham 1996). In the majority of Procellariiformes, males consistently have larger bills than females (Chapter 2). The structure of the bill apparently plays an important role in feeding and overall diet of seabirds (Prince 1980, Imber 1981). For example, a comparative study of the blue petrel (*Halobaena caerulea*) and dove prion (*Pachyptila desolata*), species of similar size with varying bill shape and structure, found that despite similarities in prey selection between the two species, there appeared to be little direct inter-specific competition as the blue petrel took significantly larger prey (Prince 1980). While there is no direct overlap in the timing of chick rearing, both species forage in the region during the same period of time, suggesting that dietary differences are due to prey selection rather than availability and related to variation in feeding techniques and bill structure (Prince 1980). Therefore, it is possible for sympatric species to segregate their food resources by both prey species and size.

Foraging niche segregation may also occur within species to reduce intra-specific competition. In some Procellariiformes this has been attributed to SSD (González-Solis 2004, Phillips *et al.* 2004). For example, male northern giant petrels (*Macronectes halli*) are significantly larger than females in body size and bill morphology. Males are primarily scavengers feeding on carrion in inshore waters whereas females have a much more pelagic diet suggesting that they forage further offshore (González-Solis 2004). The inter-sexual differences in bill size actually exceeded the size difference that might have been expected based on differences in overall body size, suggesting that SSD is a result of adaptations to reduce intra-specific competition for resources (González-Solis 2004). While sexual segregation in diet and foraging areas occurs in some Procellariiform species, other species show little difference in their foraging ecology (Navarro *et al.* 2009). However, even in the absence of inter-sexual differences in diet composition, dietary segregation based on prey size may still occur.

Limited information is available regarding the diet and at-sea distribution of white-faced storm petrels. Storm petrels generally feed by patterning along the surface of the water (Warham 1990). Anecdotal data on the diet of white-faced storm petrels have been opportunistically obtained from pellets regurgitated by adults during banding studies in Victoria and a study of
the New Zealand subspecies (Imber 1981). This limited dietary data has shown that the diet of white-faced storm-petrels predominately consists of pelagic crustaceans, small fish and other surface plankton (Marchant & Higgins 1990). No detailed studies on diet or foraging ecology of white-faced storm petrels in Australia currently exist. The white-faced storm petrel exhibit reversed SSD in several structural morphological measurements (1.5-2.7%), however, albeit a minute difference, males have significantly larger bill depths than females (1.7%; Chapter 2).

Here we report on the diet of white-faced storm petrels from two geographically separate breeding colonies in south-eastern Australia during two consecutive breeding seasons. This study aims to ascertain whether subtle differences in sexual size dimorphism influences diet composition and prey size selection between the sexes, and whether prey selection varies between seasons and colonies.

**Methods**

This study was conducted during the breeding season of white-faced storm petrels in the austral summers of 2006/2007 and 2007/2008. In Victoria, white-faced storm petrels are restricted to three breeding colonies: Mud Islands and South Channel Fort located within Port Phillip Bay, and on Tullaberga Island on the far-east coast of Victoria more than 400km east of Port Phillip Bay. The populations within Port Phillip Bay are unusual as they occur in an embayment and close to urbanisation. In contrast, Tullaberga Island, though near to the mainland, is in close proximity to the edge of the continental shelf in eastern Australia.

Diet samples were collected from individuals during the chick provisioning period in December/January (Underwood & Bunce 2004) at both Mud Islands (38°16’30"S, 144°45’00"E) and Tullaberga Island (37°34’00"S, 149°51’00"E). Adult storm petrels were caught at night in small hand nets or by hand on the ground as they returned to their burrows to feed their chick. Birds were weighed using a pesola spring balance (1 g) following capture. Based on the average weight range for white-faced storm petrels (56g; Underwood & Bunce 2004), individuals with a mass < 50 g were assumed to have empty stomachs and were immediately released. Diet samples were taken from the remaining birds after which their mass was again recorded. Each individual was banded with a metal alloy band supplied by the
Australian Bird and Bat Banding Study (ABBBS), to ensure that no individual was sampled more than once, so that a chick would not miss any further meals. Morphological measurements and blood samples were taken for sex determination from the majority of individuals (following methods in chapter 2). However, the sex was not able to be determined for 25 individuals, as morphological measurements do not provide sufficient certainty about the sex of the bird (Chapter 2).

Diet samples were obtained using the water off-loading technique (following Ford *et al.*, 1982 and Wilson 1984). An infant feeding tube attached to a 5ml plastic syringe was inserted into the oesophagus and the stomach of the birds. Approximately 5ml of lukewarm salt water was then gently syringed through the tube into the bird’s stomach. The bird was immediately inverted and gentle pressure applied to the stomach until the contents were regurgitated into a container. In the majority of cases this process was performed only once and appeared sufficient to allow recovering all stomach contents, as additional flushes taken initially were found not to contain any prey remains. Samples were stored in 70% ethanol for later analysis. A small number of birds regurgitated when caught or handled, and these were immediately released. Samples taken from these birds have been excluded from the analysis as voluntarily regurgitated samples have been found to be incomplete and therefore provide a biased sample of the diet (Hahn 1998).

**Diet Analysis**

Samples were sorted and identified under a dissecting microscope at varying magnifications. To assess the minimum number of prey consumed, prey individuals were counted. In the case of euphausiids, the number of individual eyes were counted and divided by two. The frequency of occurrence (FOO) of prey items was calculated as the percentage of samples in which a particular identifiable prey item was recorded. The numerical abundance (NA) was calculated as the total number of prey items found across all samples and converted to a percentage. Prey items were identified to species level in the majority of cases; however, this was not always possible as prey remains were sometimes heavily digested and too degraded. Major prey items that were intact and showing little evidence of degradation were measured (± 0.1 mm) using an eye-piece graticule under a dissecting microscope under varying magnifications.
Chapter 5 – Prey selection

Statistical Analysis
Statistical analyses were conducted using R, version 2.12.1 (R Development Core Team 2011). Principal component analysis was performed to analyse major prey items (defined as those contributing a NA of > 1%, \(n=12\)) using the princomp function in R. Other prey items were excluded since they were found in very low numbers and in only a few samples. Linear models and MANOVA analyses were conducted on the principal component scores where Eigen values were higher than 1 to determine the influence of sex, location and season on the diet of white-faced storm petrels. The size of major prey items that were measured (where NA>10%, \(n=5\)) were analysed using ANOVA and where preliminary analysis found data were not normally distributed, Kruskall Wallis chi-squared tests were used. A \(p\)-value < 0.05 was considered to be significant.

Results
A total of 107 diet samples were collected from white-faced storm petrels during the chick rearing period over two successive seasons 2006/07 and 2007/08 (70 from Mud Islands and 37 from Tullaberga Island). Of these, 15 samples (10 from Tullaberga Island & 5 from Mud Islands) contained no prey items and were excluded from further analyses. White-faced storm petrels from both locations consumed a diverse range of prey items, with their diets comprising fish, cephalopods and a range of crustaceans including amphipods, decapods, copepods and isopods. In total, 25 prey taxa were recorded and 11 taxa were present at both sites (Table 5.1). Geographical variation of prey taxa was observed, with six and eight prey taxa found only at Mud Islands and Tullaberga Island, respectively. Crustaceans were the main component of the diet of white-faced storm petrels in both males and females across both seasons (Figure 5.1). Coastal krill (Nyctiphanes australis; hereafter krill) was the most abundant prey item with a numerical abundance of 25.7% of all prey items at both locations. Post-larval fish were also important prey, particularly during the second year of this study, while cephalopods were only a minor component in both years and locations. Stomach oil was present in 79% of samples. Small pebbles and/or quartz pieces were found in 50% of all diet samples. Man-made objects, such as plastic, occurred in 14% of all samples, with 18.8% of samples from Mud Islands containing these objects. Only one man-made item was found (FOO 3.6%) at Tullaberga Island. Of the Mud Island birds with samples containing man-made objects, 28% were females while 17% were males.
Table 5.1 Diet composition of white-faced storm petrels (*Pelagodroma marina*) on Mud Islands and Tullaberga Island, Victoria, Australia, showing the frequency of occurrence (FOO), numerical abundance (NA), and percentage of each, for prey items from diet samples at each location separately and combined.

<table>
<thead>
<tr>
<th></th>
<th>MUD ISLANDS $n = 64$</th>
<th>TULLABERGA $n = 28$</th>
<th>Locations combined $n = 92$</th>
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<td></td>
</tr>
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<td>Post-larval Fish</td>
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<tr>
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<td>Unidentified Amphipod</td>
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<td>21</td>
</tr>
<tr>
<td>Copepod (Order Calanoida)</td>
<td>34</td>
<td>53.1</td>
<td>251</td>
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</table>

Locations combined:
- **MUD ISLANDS**: $n = 64$
- **TULLABERGA**: $n = 28$
- **Locations combined**: $n = 92$
### Crustaceans continued

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Abundance</th>
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<th>Biomass</th>
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<th>Biomass %</th>
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<th>Biomass %</th>
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<td>2</td>
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### Miscellaneous

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<th>Biomass %</th>
<th>Biomass %</th>
<th>Biomass</th>
<th>Biomass %</th>
<th>Biomass %</th>
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<td>0.2</td>
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<td>10.7</td>
<td>20</td>
<td>1.1</td>
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<td>6</td>
<td>21.4</td>
<td>10</td>
<td>0.5</td>
<td>7</td>
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</table>
Figure 5.1 Percentage numerical abundance of major components of the diet of white-faced storm petrels (*Pelagodroma marina*) by prey group at both Mud Islands (MI) and Tullaberga Island (TI) where A) shows the differences between the sexes and B) the difference between years.
In a principal component analysis on the 12 most abundant prey items (NA >1%) the Eigen values of the first four principal components were greater than one. Linear models of these first four components found that only component 2 was significantly different from component 1 in the interaction between location and season (Table 5.2) suggesting the effect of season on diet varies with location. MANOVA of the principal component scores of the first 4 components also showed significant differences in the diet between locations, seasons and the interaction between location and season (Table 5.3; Figure 5.2).

**Table 5.2** Linear models comparing component 1 and 2 from the principal components analysis of the 12 most important prey items found in white-faced storm petrel (*Pelagodroma marina*) diet from Mud Islands and Tullaberga Island (TI), Australia, during the 2007 and 2008 breeding seasons. (* indicates significance)

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>0.24</td>
<td>0.88</td>
<td>0.28</td>
<td>0.78</td>
</tr>
<tr>
<td>Location TI</td>
<td>4.62</td>
<td>1.25</td>
<td>3.69</td>
<td>&lt; 0.01*</td>
</tr>
<tr>
<td>Season</td>
<td>1.67</td>
<td>0.82</td>
<td>2.03</td>
<td>&lt; 0.05*</td>
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<tr>
<td>Sex:Location TI</td>
<td>-0.95</td>
<td>0.57</td>
<td>-1.65</td>
<td>0.10</td>
</tr>
<tr>
<td>Sex:Season</td>
<td>0.33</td>
<td>0.58</td>
<td>0.57</td>
<td>0.57</td>
</tr>
<tr>
<td>Location TI:Season</td>
<td>-2.54</td>
<td>0.61</td>
<td>-4.20</td>
<td>&lt; 0.01*</td>
</tr>
</tbody>
</table>

**Table 5.3** Manova of the principal components analysis scores of the first 4 components of the 12 most important prey items found in white-faced storm petrel (*Pelagodroma marina*) diet from Mud Islands and Tullaberga Island, Australia, during the 2007 and 2008 breeding seasons. (* indicates significance)

<table>
<thead>
<tr>
<th></th>
<th>Approx. F</th>
<th>df</th>
<th>p Value</th>
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<tbody>
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<td>1.26</td>
<td>4, 57</td>
<td>0.28</td>
</tr>
<tr>
<td>Location</td>
<td>8.73</td>
<td>4, 57</td>
<td>&lt; 0.01*</td>
</tr>
<tr>
<td>Season</td>
<td>7.93</td>
<td>4, 57</td>
<td>&lt; 0.01*</td>
</tr>
<tr>
<td>Sex:Location</td>
<td>0.72</td>
<td>4, 57</td>
<td>0.58</td>
</tr>
<tr>
<td>Sex:Season</td>
<td>0.39</td>
<td>4, 57</td>
<td>0.82</td>
</tr>
<tr>
<td>Location:Season</td>
<td>5.35</td>
<td>4, 57</td>
<td>&lt; 0.01*</td>
</tr>
</tbody>
</table>
Figure 5.2 Principal component analysis of the first two principal components of the major prey components in the diet of white-faced storm petrels (*Pelagodroma marina*) in Victoria, Australia during the 2006/2007 and 2007/2008 breeding seasons. ○ = Mud Islands, Season 1, △ = Mud Islands Season 2, + = Tullaberga Island Season 1, × = Tullaberga Island Season 2, where symbol colour represent males (red) and females (black), respectively.
Chapter 5 – Prey selection

The mean size of prey found in the white-faced storm petrel diet ranged from 3.30 mm (Ovalipes sp, megalopa) to 22.24 mm (Palaemonetes atrinubes, decopod; Table 5.4). The size ranges of the five key prey species (with a NA >1%) were studied in more detail (Figure 5.3). There was a significant interaction between sex and location ($F=3.96$, $p<0.05$) for krill. There were significant inter-sexual differences in prey size, with male storm petrels consuming larger krill compared to females ($F=15.00$, $p<0.05$). No seasonal differences in krill size were observed. Females targeted significantly larger individuals of the hyperiid amphipod (Themisto australis; $F=14.62$, $p<0.05$; Mud Islands only) (Figure 5.3). On Tullaberga Island, male storm petrels appeared to have targeted a wider size range of the euphausiid (Thysanoessa sp), whereas females had a restricted range of sizes of this species in their diet. However the mean size was not significantly different ($F=0.88$, $p=0.35$; Figure 5.3).

Geographical differences in dietary prey size were also found. There were significant differences in size of both Decapods Palaemonetes atrinubes and Ovalipes sp. between locations ($\chi^2=4.43$ & 5.75 respectively, $p<0.05$). In addition, there were significant seasonal differences in the size of P. atrinubes ($\chi^2=10.63$, $p<0.05$) in the storm petrel diet at Mud Islands.

Discussion

Diet Composition

Many seabird species have also shown considerable flexibility to seasonal and annual variations in prey availability (Warham 1996). We found that the diet of white-faced storm petrels primarily comprises crustaceans and fish, with cephalopods being of less importance. This is similar to other studies of storm petrels where crustaceans and fish also represent a high proportion of the diets of black-bellied storm petrels (Fregetta tropica, Hahn 1998) and Wilson’s storm petrel (Oceanites oceanicus; Quillfeldt 2002). Although both locations in this study had several prey taxa in common, there were also a number of unique taxa at each site, demonstrating the white-faced storm petrel can adapt to feed on locally available prey.
Figure 5.3 Prey size of the five most important prey items from the diet of white-faced storm petrels (*Pelagodromomarina*) in Victoria, Australia. Boxplots indicate median, quartiles (boxes), range (whiskers) and outliers (stars), where white boxes represent females (F) and grey boxes represent males (M) at either MI=Mud Islands or TI=Tullaberga Island or during the 2006/2007 (1) or 2007/2008 (2) breeding season.
Table 5.4 Mean length (± SE) and size range of the five most important prey items found in white-faced storm petrel \( (Pelagodroma marina) \) diet from Mud Islands and Tullaberga Island, Australia, during the 2007 and 2008 breeding seasons.

<table>
<thead>
<tr>
<th>Prey Species</th>
<th>Mud Islands</th>
<th>Tullaberga Island</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( n )</td>
<td>Mean ± SE (mm)</td>
</tr>
<tr>
<td>\textit{Nyctiphanes australis}</td>
<td>107</td>
<td>15.9 ± 0.17</td>
</tr>
<tr>
<td>\textit{Palaemonetes atrinubes}</td>
<td>37</td>
<td>14.8 ± 0.40</td>
</tr>
<tr>
<td>\textit{Ovalipes sp.}</td>
<td>174</td>
<td>6.4 ± 0.11</td>
</tr>
<tr>
<td>\textit{Thysanoessa sp.}</td>
<td>206</td>
<td>7.2 ± 0.08</td>
</tr>
</tbody>
</table>
The differences in diet composition between study sites suggest that individuals from Mud Islands and Tullaberga Island are indeed foraging in different locations and probably represent differential prey availability in the foraging areas of the two colonies. From a geographical perspective it is most likely white-faced storm petrels from Mud Islands travel a greater distance to forage in the productive waters of the edge of the continental shelf, although some birds are occasionally observed feeding just outside Port Phillip Bay (Marchant & Higgins 1990). In contrast, white-faced storm petrels on Tullaberga Island are much closer to the eastern edge of the continental shelf and, therefore, may not have to travel as far to reach productive waters.

The diversity in diet of white-faced storm petrels (*Pelagodroma marina maoriana*) was similar to that found in New Zealand, but a more diverse diet than that of the grey-backed storm petrel (*Garrodia nereis*, Imber 1981) suggesting white-faced storm petrels are more opportunistic in their prey selection than the former species. Various krill species have been found to be the most important food item in the diet of many Procellariiformes (Croxall *et al.* 1997, Quillfeldt 2002, Schumann *et al.* 2008) and white-faced storm petrels in this study are seemingly no exception, with krill the most abundant prey item. Krill is a relatively abundant shelf species and occurs throughout Bass Strait. Krill plays a key role in the food webs of Bass Strait with more than 10 species of seabirds consuming it, while some species are occasional predators; species such as the short-tailed shearwater are dependent on krill (O’Brien 1988). Generally krill are only found near the surface at night, although large diurnal, surface swarms are also a common phenomenon (Blackburn 1980). Previous studies of Wilson’s storm petrel found that the amount of krill in their diet decreased as the breeding season progressed (Quillfeldt 2002). Variation in diet composition in white-faced storm petrels during the incubation phase still remains to be assessed, but if the trend found in Wilson’s storm petrel also applies, krill may actually make up an even larger proportion of their diet over the entire breeding season than what appears from our study.

**Prey size selection**

While there were no significant differences in diet composition between male and female white-faced storm petrels, we found significant differences in the size of five key prey items consumed by each sex. Schools of krill have been found to comprise of a restricted size range...
of individuals (O’Brien 1988). These differences between schools of krill suggest that male and female storm petrels could potentially select different sized krill as a result of differences in their feeding apparatus, with males having greater bill depths than females (Chapter 2). Morgan and Ritz (1982) reported that short-tailed shearwaters (Ardenna tenuirostris) took a limited size range (similar to that of storm petrels in this study) of krill despite a range of sizes being available to them, potentially owing to the size of their feeding apparatus. However, they did not test for variation in bill size and prey-size selection between the sexes. Interestingly, the mean size of krill taken by white-faced storm petrels (this study) was greater than those consumed by shearwaters (15.9 and 13.7, respectively; Morgan and Ritz 1982, this study) despite shearwaters being much larger than the storm-petrels. This may also be a consequence of differences in the bill morphology of the two species. Like white-faced storm petrels, Cory’s shearwater (Calonectris diomedea) exhibit sexual size dimorphism in a range of bill measurements, although studies of the foraging areas and trophic level (via stable isotope signatures) have revealed no difference in diet between the sexes of Cory’ shearwaters (Navarro et al. 2009). However, diet composition and prey size were not examined as part of their study.

Seabirds exhibit extreme life history traits and have developed many strategies to reduce competition between and within species (Warham 1996). Many Procellariiformes utilise a dual foraging strategy during chick rearing, whereby they alternate between short 1-2 day and longer 3-8 day foraging trips (Weimerskirch et al. 1997, Baduni & Hyrenbach 2003). The white-faced storm petrel may also utilise this strategy (Chapter 4). This strategy allows individuals to exploit distant, productive foraging grounds to maintain individual condition as well as efficient provisioning of chicks (Weimerskirch et al. 1994, Ochi et al. 2010). Differences in foraging strategies may influence the type and size of prey available to individuals. Although not a significant proportion of the diet, three prey species were unique to the diet of females (i.e. Themisto australis, Cyllopus magellanicus (Tullaberga Island), and Sprattus novaehollandiae (Mud Island)) while the isopod, Eurydice tarti, was found only in the diet of males at both locations. White-faced storm petrels utilise different foraging strategies throughout the breeding period, with males undertaking a greater proportion of short trips compared to females who tend to make longer trips (Chapter 4). In addition, there is evidence to suggest differences in foraging distributions between the sexes during the non-breeding period (Chapter 6). These differences
in foraging strategies and diet strongly suggest that birds are also foraging in different areas. This would allow the two sexes to avoid direct competition for resources.

**Ingestion of plastics**

The potential consequences of ingestion of marine debris by seabirds falls into three categories: physical damage to the digestive tract, impairment of digestion and foraging efficiency, and the release and accumulation of toxic chemicals (Ryan 1987, Baker et al. 2002). High amounts of plastic have previously been reported in the stomachs of white-faced storm petrels and other Procellariiformes. Furness (1985) suggested that the small and constricted gizzard size in Procellariiformes may make them more susceptible to accumulation of plastics. Ingestion of plastic by white-faced storm petrels in this study was lower than in previous studies of this species (18.8% compared to 84% FOO white-faced storm petrels from Gough Island, $n=19$; Furness 1985). Interestingly, white-faced storm petrels from the Mud Islands colony had much higher amounts of man-made objects compared with those from Tullaberga Island, presumably due to their close proximity to urbanisation. The FOO of plastic was also higher in females than in males. As these samples were collected during the breeding season, it is likely that these birds were returning to feed chicks. Recently, Carey (2011) found that all short-tailed shearwater chicks sampled at Phillip Island, Victoria, contained plastic with an average of 7.6 particles per bird. Wilson’s storm petrel chicks in Antarctica averaged 4.4 particles per bird (van Franeker & Bell 1988). It is possible that white-faced storm petrels in the present study consumed greater amounts of man-made objects than indicated in diet samples since these were collected well into the chick rearing period, and individuals may have already offloaded these objects into their chicks. Nevertheless, these man-made objects are likely to pose serious consequences to the long-term survival of individual storm petrels.

**Conclusion**

Reducing inter-sexual competition for resources can have positive flow-on effects to breeding success. White-faced storm petrels could potentially reduce competition between the sexes through differences in prey species, prey size and foraging range. We did find some instances of differences in prey-species composition between the sexes of white-faced storm petrels. In addition, we did also found intersexual differences in prey-size selection, an often overlooked aspect in similar dietary studies. The observed small but significant dietary segregation between
male and female white-faced storm petrels may be driven by sexual size dimorphism. Although differences in bill size are minute, they may be the driving factor in the dietary segregation observed in the present study.
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References


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Chapter 6

Using stable isotopes to investigate a potential migratory divide for white-faced storm petrels (*Pelagodroma marina*) from Victoria, Australia

Photo by Rohan Clarke
Abstract

The year-round distribution of migratory species is an essential aspect of their ecology and understanding this is of critical importance for their conservation. Stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ can be used as a tool to assist in determining non-breeding distributions of migratory species. The white-faced storm petrel (*Pelagodroma marina*), is a small Procellariiforme that has undergone substantial declines in population numbers in Victoria, Australia. Little is known of the migratory behaviour and non-breeding distribution of these storm petrels. We found that there were distinct differences in $\delta^{13}C$ and $\delta^{15}N$ values from feathers between breeding and non-breeding foraging grounds. Significant variation in $\delta^{13}C$ values occurred between two separate breeding colonies and thus potential variation in moulting and wintering locations. Intersexual differences in $\delta^{15}N$ values in white-faced storm petrels suggest differences in trophic level and accordingly, diet. In addition, this study provides evidence of a potential migratory divide of white-faced storm petrels from two breeding colonies in Victoria.

Introduction

Seabirds spend the majority of their life at sea, returning to land only to breed. While seabird ecology during the breeding season is increasingly well documented, relatively little is known of their ecology and movements during the non-breeding period, particularly for migratory seabirds such as Procellariiformes (albatrosses and petrels). Events at non-breeding grounds have the potential to affect the population dynamics of species at their breeding grounds as well as possibly impacting on breeding strategies and reproductive success of individuals (Marra *et al.* 1998, Webster & Marra 2005). Understanding the connectivity of the breeding and non-breeding grounds of migratory species is an extremely important aspect of the overall ecology of the species and is essential for species conservation (Phillips *et al.* 2005, Webster & Marra 2005).

The white-faced storm petrel (*Pelagodroma marina*) is a small Procellariiform. Taxonomically there are six sub-species within this group that breed in both the northern and southern hemispheres (Warham 1990). Those that breed in the north do not undertake a full migration but disperse from breeding areas during winter (Warham 1990). In contrast, the Australian
subspecies, *P. marina dulciae*, undertakes a full trans-equatorial migration. While birds from colonies in Western Australia are known to winter in the northern Indian Ocean and Arabian Sea (Warham 1990), the migration of the south-eastern Australian populations remains unclear. There is some urgency in filling this knowledge gap since populations of white-faced storm petrels in south-eastern Australia have undergone significant declines. At Mud Islands the population has declined from an estimated 22,000 pairs in 1928 to approximately 5,600 pairs in 1978 (reviewed in Menkhorst et al. 1984) and less than 2,500 pairs in 2007 (M. Underwood, unpubl. data). At Tullaberga Island the current population status is unknown, although appear to also have declined (M. Underwood, unpubl. data).

Two possible migration routes of white-faced storm petrel populations in south-eastern Australia have been proposed. Firstly, they may migrate to the west, as the Western Australian populations do, and spend the non-breeding season in the northern Indian Ocean and Arabian Sea (Serventy et al. 1971). Alternatively, like the New Zealand subspecies, *P. marina maoriana*, they may head north to north-east to the tropical areas of the Pacific Ocean (Imber 1981). In Victoria, in south-east Australia, there are three colonies of white-faced storm petrels in two different regions: Mud Islands and South Channel Fort, both in Port Phillip Bay, and Tullaberga Island in far eastern Victoria over 400km east of the Port Phillip Bay colonies. Where these birds go during the non-breeding period is largely unknown. Despite over 12,500 birds banded on Mud Islands between 1955 – 1980, very few long-distance recoveries have been made. Most notable is an unofficial record of an individual found on a ship off Western Australia, suggesting that this population may migrate to the west (Menkhorst et al. 1984).

Conversely, based on a beach-washed, banded white-faced storm petrel in New Zealand, Imber (1984) suggested that the most likely wintering ground for these storm petrels from eastern Australia is the south west Pacific. It is also possible that both theories are correct and that birds in the two regions of Victoria undertake different migration routes. Such patterns have previously been reported in seabirds. For example, flesh-footed shearwaters (*Puffinus carneipes*) breeding in Western Australia and Lord Howe Island migrate in different directions (Serventy et al. 1971). Similar migratory divides have been shown to occur in the willow warbler (*Phylloscopus trochilus*) where two populations in close proximity migrate in opposite directions (Bensch et al. 1999). The white-faced storm petrel breeding in Victoria may provide yet another example of a migratory divide.
Stable isotopes of carbon ($\delta^{13}$C) and Nitrogen $\delta^{15}$N can provide a tool to assist in discerning the patterns of movement and migration of animals (Bensch et al. 1999). Values of the $\delta^{13}$C isotope have been found to increase with latitude across all of the southern oceans, providing valuable insights into the at-sea distribution of some marine animal species (Cherel & Hobson 2007). Values of $\delta^{13}$C and $\delta^{15}$N in feathers of seabirds represent those of prey and trophic information at the time of feather synthesis (Cherel et al. 2000). This can therefore, provide insights into the distribution of seabirds during the period where feathers are re-grown (Cherel et al. 2000). Stable isotope values in feathers have previously been used to identify movements consistent with migration to more tropical waters of Leach’s storm petrel ($Oceanodroma leucorhoa$) between the breeding & non-breeding season (Hedd & Montevecchi 2006).

Here we use stable isotopes as a tool to investigate the migratory behaviour and non-breeding range of white-faced storm petrels breeding in Victorian waters. To determine whether stable isotopes of feathers enable accurate differentiation of foraging distributions, we firstly compared $\delta^{13}$C and $\delta^{15}$N in feathers of chicks and adults from Mud Islands. Isotopic values of $\delta^{13}$C and $\delta^{15}$N in feathers of adults from both Mud Islands and Tullaberga Islands were then compared to investigate the potential existence of a migratory divide. White-faced storm petrels are known to exhibit sexual size dimorphism (Chapter 2), and differences in foraging behaviour and prey selection during the breeding season have been found (Chapter 4 & 5). Therefore, we also investigated potential segregation in wintering diet (and range) between the sexes during the non-breeding season. Although we apply this technique in the absence of good reference values for the hypothesised potential wintering areas, this study may at least shed light on potential segregation of over-wintering areas exploited by Victorian white-faced storm petrels.

**Methods**

This study was undertaken during the 2006/2007 breeding season at Mud Islands, Port Phillip Bay (38°16’30”S, 144°45’00”E), and Tullaberga Island (37°34’00”S, 149°51’00”E), Victoria, Australia. Geographically these islands are separated by just over 400 km. White-faced storm petrels, as with most Procellariiformes (Warham 1990), tend not to moult their feathers during
the breeding period. Previously, birds caught at sea in May were in wing moult (Imber 1984), while another bird caught in July was completing the final stages of tail feather moult (Harris & de Vries 1968). This supports observations at breeding colonies and confirms that storm petrels most likely undertake flight feather moult during the non-breeding period. As feathers are metabolically inert, the isotopic signatures of these are a reflection of prey at the time of moult (Hobson & Clarke 1992). We collected the inner-most primary feather from a 17 adults at Mud Islands and 21 adults from Tullaberga Island to provide isotope values from the non-breeding grounds. In addition we collected the inner-most primary feather from 17 chicks (Mud Islands only) to provide a comparison of the isotope values of feathers from birds at the breeding grounds. Adults were caught in small hand nets at night and chicks were taken from burrows. Blood samples were also taken for genetic sex determination (following chapter 2).

**Stable Isotope Analysis**

Feathers were taken from storm petrels using tweezers and stored in plastic tubes. Feathers were washed in a 2:1 chloroform:methanol solution to remove lipids, dried for 48 hours at 60°C, and then finely ground. Samples were analysed for δ¹⁵N (‰ difference from the ¹⁵N/¹⁴N ratio in atmospheric N₂) and for δ¹³C (‰ difference from ¹³C/¹²C ratio in Vienna PeeDee limestone) at the Environmental Biology Group Stable Isotope Facility, School of Biological Sciences, Australian National University. Based on six replicate measures the error of δ¹³C and δ¹⁵N measurement was estimated at ≤ 0.2 and ≤ 0.3 ‰, respectively.

**Statistical Analysis**

Statistical analysis was conducted using R, version 2.12.1 (R Development Core Team 2011). Prior to comparisons of δ¹³C and δ¹⁵N values between locations and sexes all data were transformed using a box-cox transformation in order to achieve normality. Where normality of the data through transformation could not be achieved or where variances were not homogenous (following Levene’s F test for homogeneity of variance), the Kruskall Wallis test was used. Otherwise, ANOVA tests were used to investigate the effects of sex, location and sex × location on isotope ratios. A p-value of less than 0.05 was considered to be significant in all statistical tests.
Chapter 6 – Migration

Results

There was a considerable difference in the stable isotope values between white-faced storm petrel chicks and adults from Mud Islands (Table 6.1; Figure 6.1). The $\delta^{13}C$ values were significantly lower in chicks than in adult white-faced storm petrels ($\chi^2=34.71, p<0.05$). However, there was no significant difference in $\delta^{15}N$ values ($\chi^2=0.18, p<0.05$). Both the $\delta^{13}C$ and $\delta^{15}N$ values appear to be much more restricted in white-faced storm petrel chicks than in those values from the adults (Figure 6.1).

Values of $\delta^{13}C$ and $\delta^{15}N$ varied greatly between storm petrels on Mud and Tullaberga Islands (Table 6.1, Figure 6.1). While mean $\delta^{13}C$ values did not differ significantly between adults from either population. There was a significant interaction in the variances of each group for sex and location ($F_{\text{ANOVA}}=9.78, p<0.05$) in $\delta^{15}N$ values. Individuals from Mud Islands show greater variation in values than individuals from Tullaberga Island ($F_{\text{ANOVA}}=7.56, p<0.05$).

Further analysis of individual locations revealed female white-faced storm petrels from Tullaberga Island had significantly higher $\delta^{15}N$ values than males ($F_{\text{ANOVA}}=6.14, p=0.02$). Although not significant, there was a tendency towards the opposite trend on Mud Islands, with males having higher $\delta^{15}N$ values than females ($F_{\text{ANOVA}}=4.24, p=0.057$). While females showed this extreme variations, male adult white-faced storm petrels from both locations had similar $\delta^{15}N$ values (Table 6.1; Figure 6.1).

Overall, there was considerable variation in $\delta^{13}C$ and $\delta^{15}N$ values between chicks and adults, and between adult white-faced storm petrels from both Mud Islands and Tullaberga Island (Figure 6.1). In addition, there was also variation in $\delta^{13}C$ and $\delta^{15}N$ values between both male and female white-faced storm petrels from both colonies (Figure 6.1).
Table 6.1 Mean (± SD) and range of δ\textsuperscript{13}C and δ\textsuperscript{15}N values in feathers of white-faced storm petrels (*Pelagodroma marina*) adults from two breeding colonies in Victoria, Australia, Mud Islands and Tullaberga Island, and for chicks from Mud Islands.

<table>
<thead>
<tr>
<th>Isotope</th>
<th>Location</th>
<th>Sex</th>
<th>n</th>
<th>Mean</th>
<th>± SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>δ\textsuperscript{13}C</td>
<td>Mud Islands</td>
<td>Adults</td>
<td>♂♀</td>
<td>17</td>
<td>-18.08</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>10</td>
<td>-18.41</td>
<td>0.88</td>
<td>-19.5 – -17.0</td>
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<tr>
<td></td>
<td></td>
<td>♀</td>
<td>7</td>
<td>-17.61</td>
<td>0.70</td>
<td>-18.8 – -16.8</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chicks</td>
<td>♂♀</td>
<td>17</td>
<td>-20.27</td>
<td>0.19</td>
<td>-20.5 – -19.9</td>
</tr>
<tr>
<td></td>
<td>Tullaberga Island</td>
<td>Adults</td>
<td>♂♀</td>
<td>21</td>
<td>-17.62</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>8</td>
<td>-17.49</td>
<td>0.67</td>
<td>-18.4 – -16.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>11</td>
<td>-17.69</td>
<td>0.38</td>
<td>-18.2 – -16.8</td>
</tr>
<tr>
<td>δ\textsuperscript{15}N</td>
<td>Mud Islands</td>
<td>Adults</td>
<td>♂♀</td>
<td>17</td>
<td>13.48</td>
<td>1.70</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>10</td>
<td>14.13</td>
<td>1.56</td>
<td>11.1 – 16.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♀</td>
<td>7</td>
<td>12.56</td>
<td>1.54</td>
<td>10.9 – 15.3</td>
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<tr>
<td></td>
<td>Chicks</td>
<td>♂♀</td>
<td>17</td>
<td>13.97</td>
<td>0.59</td>
<td>12.9 – 14.9</td>
</tr>
<tr>
<td></td>
<td>Tullaberga Island</td>
<td>Adults</td>
<td>♂♀</td>
<td>21</td>
<td>14.39</td>
<td>1.36</td>
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<td></td>
<td></td>
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<td>8</td>
<td>13.88</td>
<td>1.03</td>
<td>12.8 – 15.2</td>
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<tr>
<td></td>
<td></td>
<td>♀</td>
<td>11</td>
<td>15.05</td>
<td>1.01</td>
<td>13.0 – 16.3</td>
</tr>
</tbody>
</table>
Figure 6.1 Scatter plot of $\delta^{13}C$ and $\delta^{15}N$ isotopes of white-faced storm petrel adults from Mud Islands (squares) and Tullaberga Island (circles) and chicks from Mud Islands (triangles). Filled and open shapes represent males and females, respectively. Red lines indicate standard deviational ellipses for each group.
Discussion

We found a clear distinction in $\delta^{13}C$ values in feathers from white-faced storm petrel chicks at Mud Islands, which represent the breeding period and feathers from adults at Mud Islands which represent the non-breeding season. In addition there were also differences in the $\delta^{13}C$ and $\delta^{15}N$ values of adults from both Mud Islands and Tullaberga Island, which suggest potential variation in the trophic levels that the white-faced storm petrels are feeding at during the non-breeding season.

There was a considerable range of $\delta^{13}C$ values for adults that supports the notion of the northward migration during the non-breeding period. The values are consistent with other studies of northward migration in seabirds from the southern ocean where $\delta^{13}C$ values increase along a latitudinal gradient into more tropical waters (Cherel & Hobson 2007). There is no known correlation between stable isotope values and longitude. Moreover, there are no reference values for the two potential alternative non-breeding areas in the northern Indian and tropical Pacific Ocean. Thus, while our $\delta^{13}C$ data in adult feathers clearly indicate a northward migration in white-faced storm petrels from their Victorian breeding grounds, the precise direction remains unknown. However, the marked differences in the isotopic signatures of birds from each location and between the sexes may indicate differences in diet and possibly wintering grounds.

White-faced storm petrels adults from Mud Islands show a large range of $\delta^{13}C$ values compared to individuals from Tullaberga Island where values and, correspondingly, the likely non-breeding distribution may be more restricted. This suggests that Mud Island birds are undertaking feather moult in areas that are not visited by birds from Tullaberga Island. During the breeding period, white-faced storm petrels from both colonies show considerable variation in their diets suggesting there may be some segregation of foraging areas (Chapter 5). Consequently, it is possible that these differences in distributions also reflect segregation of foraging areas throughout the non-breeding period.

Variation in diet and foraging strategies can occur between and within seabird species as a way of reducing competition for marine resources throughout the breeding and non-breeding period (Fairbairn 1997). Sexual segregation of foraging areas of Procellariiformes during the
breeding period has previously been confirmed by stable isotope analysis of blood samples (Forero et al. 2005, Quillfeldt et al. 2008). In a study of 14 Procellariiform species during the non-breeding period, δ¹³C values were found to be greater in females than males (Phillips et al. 2009). Since there were no intersexual differences in δ¹⁵N values, it was suggested that sexes differed in their distribution (based on δ¹³C differences) but not in their trophic positions (Phillips et al. 2009). Male and female white-faced storm petrels from Tullaberga Island had significantly different feather δ¹⁵N values, indicating differences in diet. However, these differences were small and unlikely to reflect foraging at different trophic levels since the difference in δ¹⁵N values between trophic levels is in the order of 3.5 ‰ (Minagawa & Wada 1984). Intersexual differences are consistent with differences in foraging behaviour during the breeding season (Chapter 4). In addition, both sexes target different sized prey items, potentially influencing the δ¹⁵N values found here (Chapter 5). While these intersexual differences may indicate differences in diet and/or non-breeding foraging location, the fact that both effects act simultaneously can not be discounted.

This study provides a snapshot of isotope δ¹³C and δ¹⁵N values of white-faced storm petrels during a single season. Further research into seasonal and individual variation is needed to provide a greater understanding of the migratory patterns of white-faced storm petrels. As research into stable isotopes continues, an increasing knowledge base will enable the development of isoscapes for the marine environment that may further elucidate the results presented in this study. As tracking technology continues to evolve, it may also be possible to obtain more detailed information on the segregation of non-breeding foraging areas of white-faced storm petrels from south eastern Australia.
References


Chapter 7

GENERAL DISCUSSION
Sexual size dimorphism in Procellariiformes

Differences between the sexes have the ability to influence aspects of a species’ ecology significantly. The Procellariiformes are a unique order of seabirds that exhibit varying degrees of sexual size dimorphism (SSD) in both directions, being male-biased or female-biased. However, data on the smaller Procellariiformes is generally lacking. A gap in our knowledge of this fascinating order of seabirds that my colleagues and I sought to fill. This chapter provides a synthesis of our key findings, directions for future research and main conclusions of this study.

In this study we found a strong relationship with SSD and body size in Procellariiformes that changes from male-biased in the larger species to female-biased in the smaller species, as has previously been described in seabirds (Fairbairn & Shine 1993). However, bill dimorphism, the most dimorphic measurement for the majority of species, remains male-biased throughout the Procellariiformes has not previously been examined (Chapter 2). Following on from this we investigated how this pattern of SSD influenced the ecology of the small white-faced storm petrel (*Pelagodroma marina*). Female white-faced storm petrels are 0.95% - 2.76% larger than males in tarsus, wing and tail lengths. While male bills are 1.7% deeper than female’s. We found that the SSD exhibited in adults was also present in chicks prior to fledging, although this did not appear to influence the growth rate, meal size or provisioning rates for either sex (Chapter 3). Ultimately this suggests that there is no advantage (or disadvantage) to adult white-faced storm petrels in raising a chick of a particular sex.

Of particular interest in our study are the differences in ecology between male and female white-faced storm petrels. We found differences in foraging strategies between male and female white-faced storm petrel with males undertaking a greater proportion of shorter foraging trips throughout the breeding period (Chapter 4). In terms of diet composition there were no significant differences between the sexes, however we did find differences in the prey size selected by each sex (Chapter 5). Following the breeding season, we also found evidence to suggest potential segregation of male and female white-faced storm petrels in their wintering grounds (Chapter 6). These results provide further support to the inter-sexual niche divergence hypothesis suggesting segregation of foraging areas of male and female white-faced storm
petrels. These findings are similar, although to a lesser extent, to those found in studies of larger Procellariiformes that exhibit a greater degree of SSD (Weimerskirch et al. 1997, González-Solis 2004).

Each chapter has provided important information on the biology and ecology of the white-faced storm petrel and, given the underrepresentation of studies on small species in the spectrum, for the Procellariiformes in general. Overall it appears that two separate ecological processes are influencing the direction of SSD in white-faced storm petrels. Firstly, the large egg size in storm petrels is the largest in relation to body size of any of the Procellariiformes (Croxall 1984). Consequently females need to be as large as possible in order to produce such an egg and therefore a major potential driver of reversed SSD in the smaller Procellariiformes. These findings provide support for the dimorphic niche hypothesis as this SSD is likely to have evolved due to the specific differences between the sexes in their reproductive roles (Fairbairn 1997). Secondly, the differences found between the sexes in diet, prey selection, foraging behaviour and migration patterns suggest that there is potential segregation in food and foraging areas of white-faced storm petrels that may be influencing the dimorphism in bill size. The fact that this bill dimorphism remains male-biased in the majority of species provides support to the inter-sexual niche divergence hypothesis, as it is likely that these differences in bill morphology are a means of reducing interspecific competition in food and foraging (Selander 1966). Our findings suggest that these two hypotheses are driving the evolution and maintenance of SSD throughout the Procellariiformes.

Conservation & management implications

The current conservation status of white-faced storm petrel populations in Australia is relatively unknown. In Tasmania populations are believed to be approximately 90,000 pairs, however are considered vulnerable as they are only found at 32 localities and are sensitive to threats (Brothers et al. 2001). Our observations throughout this study suggest that in Victoria, the three white-faced storm petrel colonies all appear to be declining (Menkhorst et al. 1984, M. Underwood, unpubl. data). To what extent these populations have declined is unknown as are the drivers of these declines. Habitat destruction, disturbance, competition for nest space and
pests and diseases have all been identified as threats to smaller Procellariiformes (Brothers et al. 2001, Baker et al. 2002).

White-faced storm petrels appear to be opportunistic in their diet and utilise a wide range of food resources, therefore their decrease should then parallel any decreases in other generalists. Whilst plastics were found in the diet of the white-faced storm petrel, the occurrence was relatively low and unlikely to cause significant impacts to the population. Based on our stable isotope information the wintering range of white-faced storm petrels appears to be wide ranging. Although more detailed information on their wintering distribution and non-breeding behaviour is required, we tentatively conclude that the population decline is unlikely to be related to any off-breeding ground local phenomenon. Thus, it is likely that threats at the breeding colony itself are behind the observed declines. At Mud Islands there have been significant changes in populations of breeding birds, vegetation and increased predation of white-faced storm petrels. Human disturbance has increased at South Channel Fort with an increase in number of tour operators now accessing the island. At Tullaberga Island there also appears to be changes in vegetation and in the populations of other breeding seabirds. Despite these declines, breeding success of the Mud Islands storm petrel colony appears stable. Further information on the current population size and threats to breeding white-faced storm petrels is essential to ensure the appropriate conservation and management of this species in the future.

Future research

While this study has further increased our understanding of the ecology of the white-faced storm petrel there are still a number of gaps in our knowledge which are of importance to the future conservation of this species. The at-sea distribution of this species during both the breeding and non-breeding periods is still largely unknown. Understanding the migratory pathways between the breeding and non-breeding grounds is of particular importance to a species ecology and essential for conservation (Webster & Marra 2005). During the breeding period geolocators may be a useful tool to provide this information, however data may not be accurate enough if the species are not travelling great distances from the colony. To investigate foraging distributions during the non-breeding season may prove difficult if the retrieval of the device is necessary, as previous banding studies have returned relatively low recapture rates of
individuals at the colony (1.6%), although this was based on a single, annual weekend expedition (Menkhorst et al 1984). Consequently, more intense studies may provide higher recapture rates, and therefore the ability to retrieve geolocators or other devices attached between breeding seasons. Alternatively, as technology continues to develop, GPS/satellite transmitters may reduce in size and be suitable for studies of smaller species. The potential use of a space-based system may also be valuable in tracking movement of smaller animals such as the white-faced storm petrel (Pennisi 2011).

In this study we investigated the meal size received by chicks of each sex, however we did not determine the sex of the adult that provided the meal. In some Procellariiform species, differences in meal sizes provided have been found. For example in shy albatross (Thalassarche cauta) males have been found to provide larger meals to chicks compared to meals provided by females (Hedd et al. 2002). Given the differences in SSD and in foraging behaviour of white-faced storm petrels we would then expect the larger species, in this case the females, to be able to deliver larger meals. If so, this may lead to extra energetic costs to their condition, and thus consequences to reproductive effort and success.

The geographic separation of the white-faced storm petrel colonies at Mud Islands & Tullaberga Island warrants further investigation. In this study we found differences in diet suggesting white-faced storm petrels from these two colonies forage in different areas. We assume that the Tullaberga Island population are closer to more reliable and productive foraging grounds which may influence foraging trip duration and also effect breeding success.

**Conclusion**

So does size matter? In the case of the white-faced storm petrel, yes, it would appear so. The findings of this study make a significant contribution to further understanding how SSD influences aspects of the ecology of the white-faced storm petrel, and how this relates further across the order of Procellariiformes. We find that even minute differences in SSD in different measures appear to have significant ecological implications for the white-faced storm petrel. In addition, these findings could have implications for other Procellariiforme species that are considered to be monomorphic or exhibit minor SSD which can be overlooked.
References


