THE FORAGING ECOLOGY OF WEDGE-TAILED SHEARWATERS (*ARDENNA PACIFICA*) IN THE TROPICAL WESTERN INDIAN OCEAN

By

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Measurements taken of a Wedge-tailed Shearwater on Fouquet Island, St Joseph Atoll. Photo by: Luke Gordan | Save Our Seas Foundation

D.Z. Keys

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Declaration

I, Danielle Zuanda Keys, hereby declare that the thesis for the degree of Master of Science entitled, “The foraging ecology of Wedge-tailed Shearwaters (A*rdenna pacifica*) in the tropical Western Indian Ocean”, is my own work and that it has not previously been submitted for assessment to another university or for another qualification.

Keys

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General abstract

The distribution and abundance of prey largely influences how marine predators forage. Thus, understanding how marine predators respond to such changes becomes imperative when making decisions in marine spatial planning, especially in light of global climate change. Tropical marine systems are known for their relatively low productivity and high unpredictability of prey resources. Compared to higher latitudes, very few studies on seabirds have been implemented in the tropics.

The Wedge-tailed Shearwater *Ardenna pacifica* is an Indo-Pacific tropical seabird with a wide distributional range. However, like many other seabirds, its population numbers are currently declining. Very little is known about the at-sea distribution of Wedge-tailed Shearwaters in the tropical western Indian Ocean. Therefore, this thesis investigates the foraging ecology of Wedge-tailed Shearwaters in the western Indian Ocean by tracking the fine scale movements of individuals at sea. This study was conducted in two different oceanic environments, namely D'Arros Island and Fouquet Island, St Joseph Atoll in the Amirantes Group in Seychelles archipelago as well as Réunion Island in the Mascarene archipelago during the Wedge-tailed Shearwaters breeding seasons. Here I aimed to investigate the foraging distribution of Wedge-tailed Shearwaters on Réunion Island in relation to different stages of the breeding period. I also compared the foraging ecology of all three populations, subjected to different abiotic and biotic factors. Furthermore, I investigated foraging site fidelity in individuals and repeatability within individual flight characteristics.

To my knowledge, this is the first study to comprehensively investigate the foraging ecology of Wedge-tailed Shearwaters using global positioning system (GPS) loggers. This study demonstrated that the Wedge-tailed Shearwaters implement flexible foraging strategies throughout different stages of their breeding period and between different islands. In Réunion, during the shearwater breeding season, sexual segregation was prominent during early chick

rearing and both sexes implemented dual foraging. As suggested by previous studies, it is likely that long trips were implemented for self-maintenance, whereas multiple short trips were implemented to meet the high energetic demands of the chicks.

Several important foraging areas were identified for these Wedge-tailed Shearwaters. During incubation, shearwaters from Réunion faithfully foraged towards the south east of Madagascar near the East Madagascar Current and flew over large areas of the Mascarene Basin. During chick rearing, shearwaters significantly constricted their range closer to the colony and exploited deep waters on the south-west of Réunion Island. Shearwaters concentrated near oceanographic features such as the Pérouse Seamount (which is a known area of high productivity) as well as the Bourdonnais Ridge. There was no clear evidence for spatial or sexual segregation between individuals from the two study colonies in Seychelles during incubation and birds utilized a broader foraging range than birds from Réunion. This is likely to be the result of a large annual phytoplankton bloom which coincides with the shearwater breeding season in Seychelles, providing many foraging opportunities within the Seychelles Basin. The shearwaters from Seychelles exploited the Amirante Basin, East Somali Basin, and parts of the Seychelles archipelago. Shearwaters from D'Arros flew further east and foraged in the Mascarene Basin. Shearwaters from all populations foraged over deep, relatively unproductive waters with relatively high sea surface temperatures which are similar oceanographic features favoured by tuna.

Foraging plasticity between individuals from different colonies was observed with varying flight bearings, flight durations and the maximum distances travelled from their respective colonies. Shearwaters displayed dissimilar levels of site fidelity, where shearwaters from Réunion faithfully foraged towards south east Madagascar, while shearwaters from Seychelles foraged over a wide range over the Seychelles Basin. Foraging effort for shearwaters from Fouquet was lower than shearwaters from Reunion and they spent less time at sea and foraged closer to their colony. These difference in behaviour responses between colonies may be

advantageous to shearwaters, indicating that they may be able to respond to some level of environmental variability resulting from climate change and anthropogenic pressures.

Lastly, during chick rearing, though shearwaters showed low levels of repeatability in flight characterising, foraging site fidelity was high amongst some of the individuals. Here we see that shearwaters continuously rely on permanent features, like seamounts and possibly fish aggregating devices, which are known to attract high abundances of tuna. Shearwaters may to some extent be relying on memory to find prey in a seemingly unpredictable environment.

This study has helped us gain valuable insight about the foraging ecology of Wedge-tailed Shearwaters in the western Indian Ocean. Together with similar studies determining the at-sea behaviour of seabirds, better informed recommendations can be made to marine spatial planners as to where much needed pelagic marine protection should be implemented to preserve marine life in this fascinating part of the global ocean.

Key words: Wedge-tailed Shearwater, foraging distribution, hot-spots, tropics, sexual segregation, spatial overlap, behavioural plasticity, repeatability, site fidelity, GPS, Western Indian Ocean, Tuna, Réunion Island, D’Arros Island, Fouquet Island

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While collecting data and writing up this thesis, I have had the privilege of meeting the most incredible people and learning so much about various animal species in the tropics, not only seabirds. I witnessed first-hand the importance of conserving our wildlife and how small changes and continuous efforts of individuals can have a huge impact on our ecosystems. I could ‘do science’ with scientists who have been taught to think very differently to myself, which greatly influenced the way I look at things around me. Ultimately, I was blessed with experiencing the adventure of a life time.

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Unless someone like you cares a whole awful lot, nothing is going to get better. It's not.

Dr Seuss

How many are your works, Lord! In wisdom you made them all; the earth is full of your creatures. There is sea, vast and spacious teeming with creatures beyond number- living things both large and small.

Psalm 104: 24 - 25

CHAPTER 1

GENERAL INTRODUCTION

1.1 Conservation of marine environments and marine top predators

The world’s oceans provide countless ecosystem goods and services. In comparison to pristine ecosystems, ecosystems that experience a loss of biodiversity decrease in resilience as well as functionality (Naeem et al. 1994; Tilman and Downing 1994; Margules and Pressey 2000; Hooper et al. 2005). Despite all the benefits provided by the world’s oceans (Costanza et al. 1997), currently less than 5 % of the world’s oceans are protected, out of a suggested 10% by 2020 (Shugart-Schmidt et al. 2015). Nonetheless, there has been increasing awareness and interest of academics, policy makers and resource managers of the potential benefits of coastal marine reserves to both improve the conservation of marine biodiversity and to directly benefit fisheries (Carr et al. 2003). Yet, these protected areas mostly focus on sessile and sedentary ecosystems and organisms (Louzao et al. 2006) and very few protected areas are found in the pelagic ocean (Game et al. 2009). There is thus a need to protect more mobile, pelagic taxa and their oceanic environments (Louzao et al. 2006). To create appropriate protected areas in pelagic zones, it is essential that comprehensive data on biological, physical and socioeconomic factors which influence these systems are collected for use in conservation planning techniques (Game et al. 2009).

Pelagic ecosystems within the tropical western Indian Ocean are considered marine hotspots of biodiversity, in that they support globally significant populations of many charismatic and economically important marine top predators such as seabirds (Le Corre and Jaquemet 2005), cetaceans (Ballance and Pitman 1998), tunas, billfish (Worm et al. 2005) and sea turtles (Mancini et al. 2015). Many of these species cover thousands of kilometres each year, making it difficult to protect the full extent of their range. However, they are mostly at risk at their breeding and foraging grounds and along their migration routes (Louzao et al. 2006; Game et al. 2009). Creating protected areas that cover breeding or foraging areas, to limit the threats and stressors, can reduce the mortality and increase the fitness of marine top predators; even if only a small section is preserved, making it essential to set conservation targets in such areas (Game et al. 2009; Mancini et al. 2015).

1.2 Threats to seabirds

Seabirds are considered to be among the worlds' most threatened taxa (Butchart et al. 2004; Croxall et al. 2012). Of the estimated 350 species of seabirds, 28 % are considered globally threatened, 5 % are critically endangered and 10 % are near threatened (Croxall et al. 2012). Their major threats include the effects of invasive species (i.e. predation), human disturbance, fisheries (overfishing and bycatch) as well as chronic and catastrophic pollution (Croxall et al. 2012). Pelagic seabirds are, furthermore, considered to be noticeably more threatened than coastal seabirds. This status is largely governed by their small clutch sizes, reducing their ability to recover from threats (Croxall et al. 2012).

Several demographic and behavioural attributes of seabirds are largely governed by food availability and thus the monitoring of parameters such as population size, timing of breeding, chick growth rate and food consumption, body condition, as well as foraging distribution ultimately yields important information on the state of the marine environment (Cairns 1987; Le Corre and Jaquemet 2005; Piatt et al. 2006; Piatt and Sydeman 2007). Seabirds have thus been identified as valuable indicators of the state of the marine environment (Cairns 1987; Piatt et al. 2006; Piatt and Sydeman 2007). Furthermore, the foraging distribution of seabirds are generally indicative of areas of high productivity and biodiversity and as such, information of their at sea distribution is valuable in informing conservation-based marine spatial planning (Lascelles et al. 2012; Ronconi et al. 2012).

1.3 Seabirds in tropical environments

In comparison to higher latitudes, tropical ocean environments are less productive, which in turn influences food availability. Prey density is often relatively low, patchily distributed and unpredictable (Ashmole 1971; Au and Pitman 1986; Au and Pitman 1988; Ballance and Pitman 1999; Jaquemet et al. 2004; Weimerskirch 2007). To forage successfully, tropical seabirds implement different, often flexible, foraging strategies (Weimerskirch 2007). Generally, tropical seabirds are particularly efficient in flight, enabling them to travel long distances in search of food, using minimal energy. However, they face a trade-off as the morphological adaptations for flight are different to the adaptations for efficient swimming (Le Corre 1997; Ballance and Pitman 1999). As a result, the diving capabilities of tropical seabirds are reduced and they generally feed close to the sea surface catching prey through either surface seizing or plunge diving (Le Corre 1997; Ballance and Pitman 1999). Since most of their epipelagic prey are distributed below their average diving depths (i.e. upper 50 m of the water column) they make use of unique foraging strategies to locate and capture prey (Diamond 1978; Ballance and Pitman 1999; Weimerskirch et al. 2005b; Weimerskirch et al. 2010). They forage in multi-species flocks and have developed a ‘near obligate commensalism’ with tuna and other top predators, which drive prey to the surface within reach of the seabirds (Au & Pitman 1986; Ballance and Pitman, 1999; Jaquemet et al. 2004).

In the tropical western Indian Ocean, tuna fisheries (mostly targeting skipjack tuna *Katsuwonus pelamis,* bigeye tuna *Thunnus obesus* and yellowfin tuna *Thunnus albacares*) have rapidly been expanding since the 1980s (IOTC 2015). There have been further increases in longline and purse seine catches on an industrial scale due to advances in technology and substantial increases in fishing effort. Catches per year have further been increasing since 2012, with catches over 400 000 tones recorded per annum. Currently, according to the Indian Ocean Tuna Commission (IOTC) report in 2017, the yellowfin stocks are overfished and subject to overfishing (IOTC 2017). Although major seabird mortalities are often caused by fisheries due to accidental catches (bycatch) and overfishing (leading to competition for the same food resources; Croxall et al. 2012), this does not seem to be the case in the tropical western Indian Ocean (Le Corre et al. 2012). This is most likely due to the foraging behaviour of tropical seabirds, most of which feed on small epipelagic prey, similar to that of the top predatory fish targeted by the tropical tuna fisheries (Potier et al. 2007). Thus, the tuna fisheries and seabirds do not directly compete for the same food resources (Le Corre et al. 2003). Theoretically, by removing large subsurface top predatory fish will lead to a release of epipelagic prey which would be beneficial for the seabirds. However, this is unlikely due to the relationship between tropical seabirds and top predators in acquiring prey (Le Corre et al. 2012).

Studying and monitoring the at-sea distribution and diet of seabirds can aid in the identification of ecologically important areas. Even if they are only protected for a part of the year, reduced exposure to threats may increase their fitness (Game et al. 2009). This is especially true during the breeding season, which is very energetically demanding and seabirds face many stressors (Game et al. 2009). Very few studies have been done in the tropics, compared to temperate and polar regions (Weimerskirch 2007). Most studies on the at-sea distributions of tropical seabirds have been based on shipboard or land-based observations (Jaquemet et al. 2004, see Catry et al., 2009b) and more recently the use of satellite transmitters and light-based geolocations (e.g. Catry et al. 2009b). With the further advancement and miniaturization of technology such as miniaturized Global Positioning System (GPS), the movements of smaller seabirds can be tracked providing essential information on their foraging ecology (Cecere et al. 2013; Soanes et al. 2015). Such assessments are particularly relevant for smaller seabird species such as Wedge-tailed Shearwaters *(Ardenna pacifica*) that are known to be vulnerable to anthropogenic pressures in the Indian Ocean, while breeding as well as during the overwintering period (Catry et al. 2009b; Le Corre et al. 2012).

1.4 Study species

The Wedge-tailed Shearwater (hereafter shearwater) is an Indo-Pacific tropical seabird species with an exceptionally large distributional range of about 20 000 km^2, extending between approximately 35°N and 35°S (Harrison 1987; BirdLife International 2016). The population trend is slowly decreasing due to predation by invasive species, unsustainable levels of exploitation, persecution as well as over exploitation of by tuna fisheries (Brooke 2004). The decline, however, is not fast enough to list it as vulnerable (since the population size is so large) and it is currently listed under least concern by the IUCN Red List of threatened species (BirdLife International 2016).

Shearwaters belong to the family Procellariidae and are a medium sized, tube-nosed species and are the largest tropical shearwaters weighing between 350 – 500 g (McDuie et al. 2015). It has a characteristic ‘wedge tail’, giving rise to its name. They are colonial breeders that generally nest in deep cavities or burrows which a breeding pair excavates themselves. They have a seasonal breeding cycle which tends to be more synchronous at higher latitudes (Whittow 1997). On Réunion Island, the adults first start arriving at the colonies between July – August and synchronously start breeding during November with the young hatching in January. The adults depart late April or beginning May, approximately the same time the birds start fledging. In Seychelles, the adult birds return to breeding islands as early as May (Catry et al. 2009b) and the breeding season begins around late August to early September (Kappes et al. 2013).

The adults are sexually monomorphic and both sexes intermittently attend the colony during nest building and courtship (Whittow 1997). Both partners undertake a pre-laying exodus after mating for up to four weeks to increase energy reserves during the incubation period (Whittow 1997). Generally, a single egg is laid per breeding season and incubated for approximately 50 days. Upon hatching, the chick is brooded and this guard stage lasts up to one week. Chicks fledge when they are 100 – 115 days old (Whittow 1997; *unpublished data* LB).

During the breeding season, shearwaters in the tropical waters of Australia Great Barrier Reef have been found to employ a dual (bimodal) foraging strategy, where adults alternate several short trips (between 1 to 4 days) with a long trip (8 to 14 days), foraging between 300 and 1 100 km from the colony (Congdon et al. 2005; McDuie et al. 2015). Adults employ short trips near the breeding colony, usually in resource-poor areas to provision the chick, and forage to higher productive areas further from the colony to restore body condition after the short trips (Weimerskirch et al. 1994). Whereas in the sub-tropics, by studying adult provisioning patters, it was found that adult shearwaters employ a unimodal foraging strategy only undertaking short trips that last approximately 1.5 to 2 days (Baduini 2002; Peck and Congdon 2005). These dissimilarities in foraging and provisioning behaviour are thought to occur due to the differences in the distribution and abundance of prey resources (Baduini 2002).

During the breeding and non-breeding period, shearwaters spend a high proportion of time on the water during the night. During the day, they spend almost all their time flying (Catry et al. 2009b). Due to the close association of shearwaters and tuna, which are diurnal feeders, they too are thought to mostly forage during day (Whittow 1997; Weimerskirch 2007). Dietary studies at Aride and Cousins Islands have indicated that shearwaters predominantly feed on juvenile goat fish (Mullidae) and flying squid and some crustaceans (Catry et al. 2009a). Most diving activity in shearwaters appears to be limited to the upper 15 m of the water column (Peck and Congdon 2006), with males diving significantly deeper than females (Peck and Congdon, 2006). However, Burger (2001) indicated that they are capable of diving to depths more than 50 m, suggesting that tropical shearwaters are specialist foragers (Burger 2001). A tracking study, using geolocators on Aride Island, revealed that throughout the breeding season the birds foraged to the east of the island and avoided shallow waters of the Mascarene Plateau, foraging mostly in waters with depths ≥ 3500 m (Catry et al. 2009b).

Between breeding seasons, when not constrained by nest attendance regimes and chick provisioning, birds foraged further afield utilizing one of two strategies, either remaining in the region to the east of Aride Island, or migrating eastward to utilize foraging areas extending throughout the Central Indian Ocean, up to the Ninety East Ridge (Catry et al. 2009b). However, thus far, little is known about the fine scale foraging ecology of shearwaters breeding within this region (but see Catry et al. 2009b; Le Corre et al. 2012; Cecere et al. 2013). A more recent study, on the same shearwater colony in Aride Island, confirmed that they forage to the east of the island (117 km away for the colony; Cecere et al., 2013) however, the area exploited was smaller during the late chick-rearing phase than previously recorded 3 313 km^2 (Cecere et al., 2013) versus 160 000 km^2 (Catry et al. 2009b).

Sexual dimorphism in seabirds is known to impact their competitive abilities and foraging efficiency at sea (Lewis et al. 2005; Phillips et al. 2006; González-Solís et al. 2007). Nevertheless, sex specific foraging strategies have also identified in monomorphic species (Lewis et al. 2002; Pinet et al. 2012; Botha et al. 2017). In shearwaters, sexual segregation possibly seems to be more prominent during the breeding season where the females have a broader foraging distribution (Catry et al. 2009b) and their trips last longer (Peck and Congdon 2006) than males. Yet, this is not the case during the overwintering period where there is noticeable difference in their distribution (Catry et al. 2009b).

1.5 Study Sites

There are 30 known seabird species which breed in the tropical western Indian Ocean giving rise to an estimated 19 million breeding individuals (Danckwerts et al., 2014). These breeding seabirds are concentrated in three major areas namely, the Seychelles archipelago, Mozambique Channel and Mascarene archipelago which support approximately: 9.68, 7.69 and 1.38 million breeding individuals respectively (Le Corre et al. 2012; Danckwerts et al.

2014). Some of the major breeding grounds for the shearwaters are in the Mascarenes (229 075 breeding individuals) and Seychelles (246 075 breeding individuals; Le Corre et al. 2012; Danckwerts et al. 2014). Data was collected from D'Arros Island and Fouquet Island in the Seychelles archipelago as well as Réunion Island in the Mascarenes archipelago during the shearwaters' breeding seasons (Fig. 1.1).

1.5.1 D'Arros and Fouquet Island, Seychelles

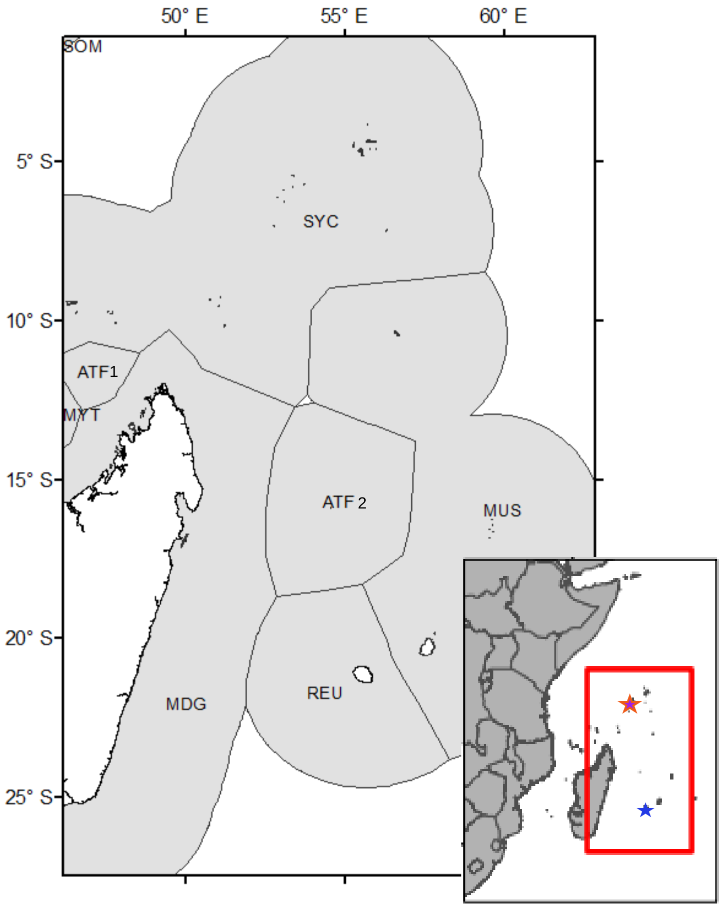


Figure 1.1 Map of the study colonies in Seychelles (★) and Réunion (★) and surrounding exclusive Economic Zones (EEZ, namely: SYC (Seychellois), ATF1 (Glorioso), MYT (Mayotte), ATF2 (Ile Tromelin), MUS (Mauritian), MDG (Madagascan), REU (Réunion).

The islands and atolls in Seychelles cover a total landmass of 445 km^2 in an economic exclusion zone (EEZ) of approximately 1 374 000 km^2 (Rocamora and Skerret 2001). There are 155 islands in Seychelles which are divided into two major groups: the granitic islands and the outer islands. The outer islands form a linear archipelago of 26 islands on a shallow bank in relation to surrounding waters which vary in depth between 11 – 70 m. These islands rarely rise above 3 m above sea level (Rocamora and Skerret 2001).

The climate in this region is seasonal and between November and March, hot and wet north-westerly winds (NW monsoon) dominate. Dryer, cooler south-easterly winds dominate between May and September (SE monsoon). This seasonality makes food availability to seabirds in Seychelles more predictable on a large scale, yet still highly unpredictable on a small temporal scale (Catry et al. 2009a). The shearwater's breeding season in Seychelles coincide with the two major phytoplankton blooms occurring in the Seychelles archipelago, the first occurring between May to August, and the second occurring between December to February (Monticelli et al. 2007; Catry et al. 2009b).

This study was undertaken on D'Arros (5°, 24'S; 53° 18' E) and Fouquet Island, St Joseph Atoll (5° 25'S; 53° 20' E) which are both coralline islands in the Amirates group. D'Arros Island is a private retreat and research centre, which is currently managed by the Save Our Seas Foundation (SOSF). The D'Arros Research centre supports conservation efforts on D'Arros Island and St Joseph Atoll. There is currently only one large house for guests who rent the island and several smaller houses that are permanently occupied by the island's staff and researchers. D'Arros Island and St Joseph Atoll are separated by a narrow channel which runs from south to north and is approximately 73 m deep (Stoddart et al. 1979). St Joseph Atoll is situated near the eastern edge of the Amarantites Ridge, east of D'Arros Island and consists of several uninhabited islands and banks that only cover approximately 1.39 km^2 (Stoddart et al. 1979). Fouquet Island, is the second largest island in the atoll and sits on the inner reef-flat margin. Fouquet Island is home to the third largest breeding colony in the western Indian

Ocean with population estimates of 28 655 breeding pairs of shearwaters (Kappes et al. 2013). Currently, the island is listed as a proposed Important Bird Area (IBA). Sadly, like many other islands, Seychelles' flora and fauna have greatly been threatened by habitat destruction, introduction of alien and invasive plants and animals and unsustainable exploitation of the fauna (Rocamora and Skerret 2001). The natural landscape of D'Arros Island and Fouquet Island in particular, have largely been influenced by coconut plantations (Stoddart et al. 1979). However, after much effort, rats (*Rattus norvegicus*) have successfully been removed from D'Arros Island (Bristol and Dunlop 2005).

1.5.2 Grand Anse, Réunion

Réunion Island (21°37'S; 55°55'E), a French territory, lies in the westernmost end of the Mascarene Island group in the tropical western Indian Ocean. It is a volcanic island with an area around 2 512 km^2. The centre of the island consists of a volcanic massif consisting of two main shield volcanoes, of which one is still active (Duncan et al. 1990). More than 60% of the island is 1 000 m above sea level and reefs and islets are largely absent around the coastline. At 10 and 30 nm from the coast the ocean depth reaches 1 500 m and 3 500 m respectively (Le Corre and Safford 2001). The island is surrounded by homogeneous oceanic environment with no nearby upwelling areas (Jaquemet et al. 2004).

The climate is dominated by tropical depressions and the south-east trade winds. The mountains in the east of the island are very humid and receive between 2000 and 5000 mm annual rainfall. The western lowlands are hotter and dryer receiving less than 2000 mm annual rainfall. High rainfall is brought by cyclones and the wettest, hottest months are between December and April during the monsoon season (Le Corre and Safford 2001).

Réunion has a high proportion of threatened and endemic taxa. It is covered by a wide variety of dry and wet shrub land and forest. Of the 546 flowering plant species described on the island 30% are endemic and over the years 592 exotic species have been introduced and have naturalised (Le Corre and Safford 2001). It is estimated that 50% of the native vertebrate species and 55% of the bird species have been driven to extinction (Mourer-Chauvire et al. 1999) and a lot of the native vegetation has been destroyed by habitat destruction and the introduction of invasive plants and animals (especially rats *Rattus rattus* and feral cats *Felis catus*; Lagabrielle et al. 2009). Currently there are eight IBAs on the island, listed under the categories A1, A2 and A4ii (Le Corre and Safford 2001). There are approximately 900 breeding pairs of Wedge-tailed Shearwaters on Réunion Island and a further 65 breeding pairs on Petite Île, a small island near this colony (Le Corre and Safford 2001). This study was conducted at Grande Anse Protected Area, where there is a relatively high density of breeding Wedge-tailed Shearwaters (personal communication Mathieu le Corre).

1.6 Rationale and motivation

This project aimed to assess the foraging ecology of Wedge-tailed Shearwaters by tracking the at-sea distributions of individuals breeding in two different oceanic environments in the tropical western Indian Ocean. The study was conducted in D’Arros Island and Fouquet Island, St Joseph Atoll in the Amirantes Group in Seychelles archipelago as well as Réunion Island in the Mascarene archipelago. Few tracking studies have concentrated on shearwaters in tropical waters (Baduini 2002; Congdon et al. 2005; Catry et al. 2009b; Cecere et al. 2013; Kappes et al. 2013) and none have utilized Geographic Positioning Systems (GPS) to determine the fine scale distribution of these shearwaters on any of the above-mentioned islands. Due to the advancement and miniaturization of tracking devices, the at sea distributions and fine scale foraging behaviour of these small seabirds can now be studied. By determining foraging hotspots of these birds, which are in high abundance in the tropical western Indian Ocean, together with similar studies on other marine top predators, suggestions can be made to marine spatial planners as to where the potential suitable pelagic marine protected areas could be implemented to protect marine life.

1.**7 Aims**

1. To investigate the foraging distribution of Wedge-tailed Shearwaters breeding on Réunion Island during incubation and early chick rearing.
2. To compare the foraging ecology of three different populations of Wedge-tailed Shearwaters breeding in D'Arros and Fouquet Island, Seychelles as well as Réunion Island.
3. Investigate repeated foraging trips and foraging characteristics of Wedge-tailed Shearwaters during early chick rearing.

1.8 Key objectives, research questions and hypotheses

Chapter 2: Foraging strategies of Wedge-tailed Shearwaters (*Ardenna pacifica*) breeding on Réunion Island, western Indian Ocean.

Objective 1: To assess the foraging distribution of incubating and chick rearing Wedge-tailed Shearwaters breeding on Réunion Island.

Objective 2: Assess potential different foraging strategies implemented by Wedge-tailed Shearwaters, in relation to **a.** sexual segregation and **b.** dual foraging.

1. **Research question:** Does the forging distribution of adult Wedge-tailed Shearwaters vary with respect to breeding period?

H 1: Based on findings from other seabirds, Wedge-tailed Shearwaters restrict their range during chick rearing (as compared to incubation) to meet the energetic requirements of their chicks.

2. **Research question:** Do the flight characteristics and foraging distributions of male and female Wedge-tailed Shearwaters differ?

H 2: Wedge-tailed Shearwaters are monomorphic seabirds, studies have shown that they show spatial segregation during chick rearing. Thus, male and female Wedge-tailed Shearwaters spatially segregate while foraging

3. **Research question:** Do Wedge-tailed Shearwaters from Réunion implement dual foraging during early chick rearing?

H 3: Like other tropical shearwaters, Wedge-tailed Shearwaters will implement dual foraging during chick rearing, thus implementing several short foraging trips before executing a single long foraging trip.

Chapter 3: Comparative foraging ecology of Wedge-tailed Shearwaters (*Ardenna pacifica*) breeding in the tropical western Indian Ocean

Objective 1: To compare the foraging distribution of incubating Wedge-tailed Shearwaters breeding on two closely situated islands in Seychelles (i.e. D'Arros and Fouquet) and an island on the edge of the tropics (i.e. Réunion Island).

Objective 2: To compare the flight characteristics of Wedge-tailed Shearwaters breeding on different tropical island in the western Indian Ocean

Objective 3: To compare foraging areas with key abiotic and biotic factors.

1. **Research question:** To what extent do the foraging distributions of Wedge-tailed Shearwaters overlap?

H 1: Due to the shifts in phenology and the large spatial gap between the populations in Seychelles and Réunion, there will be no overlap during the incubation between these populations.

H 2: To avoid intra-specific competition, foraging distributions of shearwaters from neighbouring colonies show clear spatial segregation.

2. **Research question:** How do the flight characteristics of shearwaters from separate islands differ?

H 3: Between neighbouring colonies, Wedge-tailed Shearwaters form the larger colony forage further from the colony to avoid intra-specific competition.

3. **Research question:** To what extent do Wedge-tailed Shearwaters overlap their foraging distribution with abiotic (i.e. bathometry, sea surface temperatures (SST)) and biotic factors (i.e. primary productivity)

H 4: Wedge-tailed Shearwaters forage over deep, pelagic waters, in areas of relatively high SST (consistent with tuna distributions), in areas of low productivity.

Chapter 4: Repeated foraging areas and inconsistent behaviours between individual Wedge-tailed Shearwaters (*Ardenna pacifica*)

Objective 1 To analyse repeatability in flight characteristics of individual Wedge-tailed Shearwaters performing multiple foraging trips

Objective 2 To investigate flight fidelity in consecutive foraging trips of individual Wedge-tailed Shearwaters.

1. **Research question:** Are the flight characteristics of individual Wedge-tailed Shearwaters repeatable?

H 1: Due to the dynamic nature and unpredictability of the pelagic environment, flight characteristics will show low repeatability

2. **Research question:** Do Wedge-tailed Shearwaters consecutively return to the same foraging areas (i.e. indicating high site fidelity)?

H 2: Wedge-tailed Shearwaters associate with subsurface marine top predators, like tuna, which in turn aggregate near seamounts and fish aggregating devices. Wedge-tailed Shearwaters will show high foraging site fidelity in these areas.

1.9 Research licence and ethics

In Réunion, handling, banding and equipping birds with telemetry devices was done under the authorization n° 1392 provided by CRBPO. The authorization to work at Grande Anse protected area was given by Conservatoire du Littoral Antenne Océan Indien. Permits and permissions to undertake this study in D'Arros and St Joseph Atoll. were granted by the Seychelles Ministry of Environment. All procedures performed were in accordance with the ethical standards of Nelson Mandela University (permit number: A16-SCI-ZOO-013).

1.10 Thesis outline

Succeeding the **general introduction** described above, three data chapters are introduced. I have structured the mentioned chapters of this thesis in a format that is suitable for the submission as full scientific articles, subsequently there are some overlap between sections.

In **Chapter 2,** I describe the foraging strategies of Wedge-tailed Shearwaters breeding on Réunion Island by making use of GPS loggers deployed during incubation and early chick rearing. This chapter mainly focuses on the foraging distribution of the shearwaters during different breeding stages and to what extent they show sexual segregation.

In **Chapter 3,** I compare the foraging ecology of three populations of Wedge-tailed Shearwaters from D'Arros Island, Fouquet Island and Réunion Island. I look at the differences in flight characteristics (i.e. metrics) between close neighbouring colonies as well as a colony situated near the edge of the tropics. I then assess the relationship between these metrics and potential abiotic and biotic factors influences.

In **Chapter 4,** I analysed multiple trips of individual Wedge-tailed Shearwater during early chick rearing and describe repeatability within flight characteristics and foraging fidelity in a seabird foraging in specific areas.

In **Chapter 5,** I conclude my thesis by contextualizing my findings and suggest recommendations for future research.

CHAPTER 2

FORAGING STRATEGIES OF WEDGE-TAILED SHEARWATERS (*ARDENNA PACIFICA*) BREEDING ON RÉUNION ISLAND, WESTERN INDIAN OCEAN

2.1 Introduction

Pelagic ecosystems within the tropical western Indian Ocean have been identified as hotspots of biodiversity that support globally significant populations of many charismatic and economically important marine top predators such as seabirds (Le Corre and Jaquemet 2005), cetaceans (Ballance and Pitman 1998), tunas, billfish (Worm et al. 2005) and sea turtles (Mancini et al. 2015). Information on the at-sea distribution of these marine top predators are often lacking, despite the potential of such data aiding in the identification of ecologically important areas (e.g. Reisinger et al. 2018). Once identified, such areas can feed into conservation-based marine spatial planning initiatives thereby potentially reducing threats that these animals are exposed to (Game et al. 2009).

Seabirds are among the worlds' most threatened taxa (Butchart et al., 2004; Croxall et al., 2012). The distribution and foraging trip characteristics of seabirds depend on the abundance, dispersal, mobility and predictability of their prey (Bell 1991; Baduini 2002). In addition, during the breeding season, seabirds are central place foragers and regularly commute between foraging zones and their colonies to incubate their eggs or feed their chicks. In comparison to higher latitudes, the tropics characteristically have low productivity with highly unpredictable prey resources (Ashmole 1971; Au and Pitman 1986,1988; Ballance and Pitman 1999; Jaquemet et al. 2004; Weimerskirch 2007). This places significant constraints on seabirds foraging in these waters, however, they have been found to be particularly efficient in flight, enabling them to travel long distances, using minimal energy, in search of food (Ballance and Pitman 1999; Congdon et al. 2005; Catry et al. 2009b; McDuie et al. 2015).

Seabirds have adopted the following strategies. (1) They sometimes associate with subsurface marine top predators, especially tuna, that drive epipelagic prey to the sea surface within reach of the seabirds (Au & Pitman 1986; Ballance and Pitman, 1999; Jaquemet et al., 2004). (2) They have been reported to adopt dual foraging, where individuals alternate between several short foraging trips (to collect food for chicks), before leaving on a single long foraging trip (for self-maintenance). This strategy is used by several procellariform species (Weimerskirch et al. 1994; Weimerskirch and Cherel 1998; Congdon et al. 2005; Magalhães et al. 2008; McDuie et al. 2013) to deal with the patchily distributed prey including areas of low productivity in the tropics (Congdon et al. 2005; McDuie et al. 2015). However, this strategy is likely to be colony specific and dependent on resource availability near the colony (Baduini 2002). Lastly, (3) sex-specific foraging has often been observed, mostly in many dimorphic seabird species where differences are usually associated with size related mechanisms that influence their competitive abilities and foraging efficiency (Lewis et al. 2005; Phillips et al. 2006; González-Solís et al. 2007). However, different sex related foraging strategies have also been described in monomorphic seabird species (Lewis et al. 2002; Pinet et al. 2012; Botha et al. 2017). These are thought to arise due to differences in energetic or nutritional requirements leading to differences in parental investment during chick rearing (Monaghan et al. 1998; Elliott et al. 2010).

Tropical seabirds tend to have low foraging site fidelity due to the relatively low productivity and unpredictability of tropical waters (Weimerskirch et al. 2005b; Weimerskirch 2007). However, when prey resources are associated with predictable oceanic features, like seamounts (Haney et al. 1996; Thompson 2008; Clark et al. 2010) or annual phytoplankton blooms (Pinet et al. 2012), seabirds may return to the same area making these areas important for conservation measures as well as the survival of a species (Piper 2011; Le Corre et al. 2012; Baylis et al. 2015).

In this study, I used the Wedge-tailed Shearwater (*Ardenna pacifica*) as a model species to study foraging strategies in tropical seabirds in the western Indian Ocean. The Wedge-tailed Shearwater is a monomorphic, medium sized procellariform and is one of the largest tropical shearwaters (McDuie et al., 2015). It is an ideal model species because it is relatively abundant and it has an exceptionally large distributional range, extending between approximately 35°N – 35°S and 42°E – 104°W (estimated extent of occurrence 160 million km^2; BirdLife International 2016). They are colonial breeders and generally nest in cavities or burrows (Whittow, 1997), making them relatively easy to handle. They have been found to be sensitive to spatial and temporal changes in the marine environment (Smithers et al. 2003; Peck et al. 2004; McDuie et al. 2013) and can consequently be used as an indicator of environmental change.

I aimed to evaluate the at-sea distribution and foraging strategies of Wedge-tailed Shearwaters breeding at Réunion Island. More specifically, I examined their foraging behaviour in relation to breeding stage and sex to identify important areas used by Wedge-tailed Shearwaters. Though Wedge-tailed Shearwaters are monomorphic, sex-specific foraging behaviour has been identified in this species (Peck and Congdon 2006), suggesting that it could occur across its range. Furthermore, I investigated whether the shearwaters implement unimodal or dual foraging trips. My predictions were: (1) During incubation, shearwaters will forage further from the colony than during chick rearing, since not restricted to meet the demands of the chick. (2) Though ocean productivity surrounding Réunion Island is low, I expected during chick rearing that shearwaters would implement multiple short trips near the island, to meet the energetic requirements of the chicks and forage longer and/or further from the colony (executing a single long trip) for self-maintenance.

2.2 Materials and methods

2.2.1 Study area

This study was conducted over two consecutive breeding seasons of the Wedge-tailed Shearwaters (hereafter shearwater) at Grand Anse, Réunion Island (21° 22' 30" S; 55° 34' 07" E) during the 2015/16 and 2016/17 breeding seasons. Adult shearwaters first start arriving at Grand Anse between July – August and synchronously start breeding during November with the young hatching in January. The adults depart late April or beginning May, approximately the same time the birds start fledging. There are an estimated 900 Wedge-tailed Shearwater breeding pairs on Réunion Island (*unpublished data* MLC).

Réunion Island lies in the westernmost end of the Mascarene Island group in the tropical western Indian Ocean (Duncan and Hargraves, 1990). More than 60% of the island is 1 000 m above sea level and reefs and islets are almost absent around the coastline. At 10 and 30 nm from the coast the ocean depth reaches 1 500 m and 3 500 m respectively (Le Corre and Safford, 2001). The island is surrounded by homogeneous oceanic environment with no nearby upwelling areas (Jaquemet et al., 2004; see Fig. 2.1).

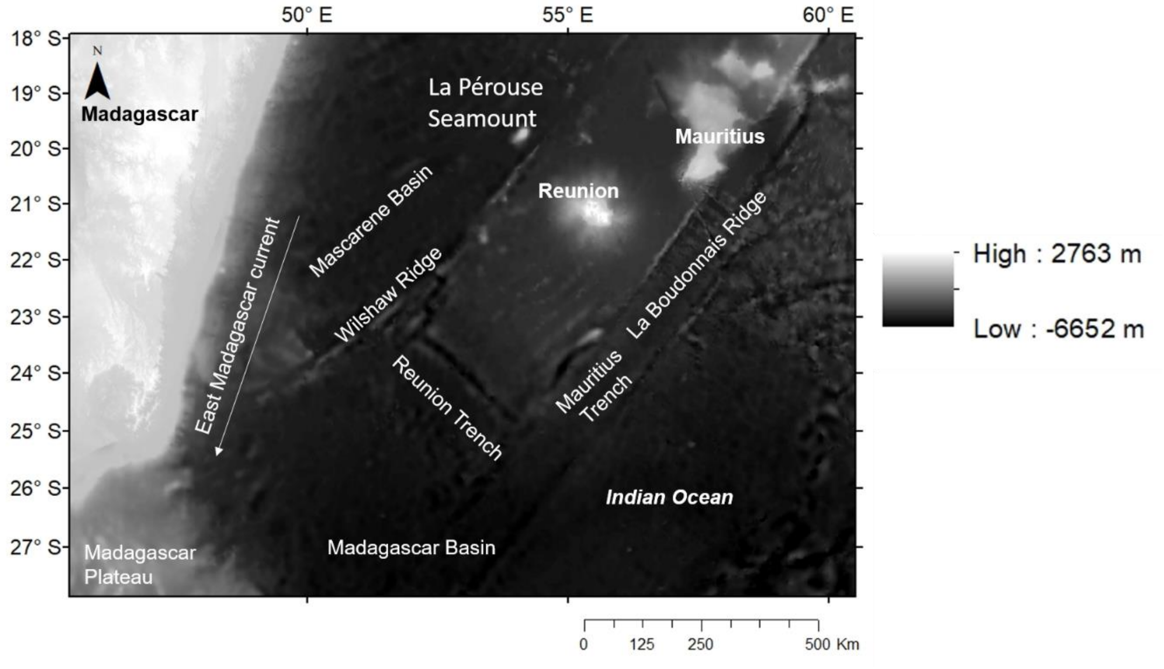


Figure 2.1. Principal oceanographic and geomorphological features around the Wedge-tailed Shearwater colony (star), scale represents the mean height above sea level (m).

2.2.2 Data collection

Data were collected between 20 January – 27 March 2016 (season one, S1) and 10 December 2016 – 27 January 2017 (season two, S2). Three different GPS models were deployed on adult birds. During S1, chick rearing shearwaters were equipped with Axy-Trek dataloggers (TDR; Axy-3™, TechnoSmArt, Rome, Italy; 30 mm x 22 mm x 10 mm, 8 g). Deployments were made during the early chick rearing (10) and late chick rearing periods (16) and loggers were programmed to log position every 20 and 60 min, respectively. During S2, birds were equipped with either CatTraQ2™ GPS loggers (Catnip Technologies, USA; 44 mm x 23 mm x 12 mm, 12 g) covered in clear heat-shrink tubing for waterproofing or the Axy-Trek dataloggers. Deployments were made during the incubation period (35 CatTraQ GPS loggers, 5 Axy-Trek GPS loggers) and early chick rearing (14 GPS CatTraQ GPS loggers and 2 Axy-Trek GPS loggers). The loggers were programmed to log position every 60 min. Loggers were attached to either the dorsal midline of the shearwater’s lower back or their tail feathers using strips of

TESA® tape (Beiersdorf AG, Germany). After modification, all loggers weighed ≤ 3.6 of the shearwaters body mass (logger + attachment = 10 – 11g; average bird mass before foraging trip = 370 g).

During the incubation period, adults that were confirmed incubating an egg and weighing < 380 g were carefully removed from their burrows and equipped with above-mentioned loggers. Relatively light birds were selected as birds lose about 10 g/day on average while incubating (*unpublished data* DZK), and were more likely to depart soon on a foraging trip (following partner changeover). These loggers were set to start recording after 2 – 4 days to avoid wasting battery life while the birds were still in the burrow. During chick rearing, adult shearwaters returned at night, fed their chicks and left their burrows shortly thereafter. Thus, burrows were monitored between 18:00 – 06:00 to locate and equip chick-rearing birds. Once an adult had finished feeding its chick and started exiting the burrow, it was carefully caught and equipped with a logger that was turned on immediately. Study birds were weighed using a spring balance (Pesola, Baar, Switzerland) with a precision of 5 g, before and after foraging trips after they fed their chick (without the device attached). They were marked on their breast- and head feathers with non-toxic white paint (Genuine Heritage Craft Products, South Africa) to quickly identify deployed birds in the burrow and to avoid disturbing their partner. To record multiple trips per individual, the loggers were retrieved after seven days of deployment. On retrieval, approximately five breast feather samples were plucked. Average handling time was kept to under eight min.

2.2.3 Molecular sexing

Approximately 3 mm of the root tip of 3 – 4 dry breast feathers per individual were used to isolate DNA using a Chelex® extraction method (Rishworth et al. 2014; adapted from Walsh et al. 1991; Ellegren 1992). The feathers were sectioned into 200 µl 5% Chelex 100 resin (BioRad) with 1 µg proteinase K. The mixture was vortexed for 20 s and then incubated at

56°C for 2 h. After 2 h, another 1 µg proteinase K was added to the mixture and vortexed for 20 s and incubation continued for a further 2 h. After 4 h of incubation at 56°C, the mixture was vortexed for 10 s and incubated at 95°C for 10 min, re-vortexed and centrifuged at 36000 RPM. The supernatant was extracted from the mixture and 1 µl of the supernatant was used to measure the DNA yield, using a NanoDrop® 2000c Spectrophotometer (Thermo Scientific). The remaining supernatant was stored at - 40°C. The 2550F (5'-GTTACTGATTC GTCTACGAGA-3') and 2718R (5'-TTGAAATGATCCAGTGCTTG-3') primers were used to amplify fragments of the sex-linked CHD-1 gene (Fridolfsson and Ellegren 1999). After amplification, these primers allow for the detection of females as two fragments (ZW) and males as a single fragment (ZZ; Appendix Fig. A).

Polymerase chain reactions (PCR) in a 15 µl solution containing: 4.3 µl of molecular grade H_2O, 7.5 µl of GoTaq® G2 Hot Start Green Master Mix (Promega), 0.6 µl; 50 nmol of each primer and 40 – 410 ng (2 µl; 50 nmol) DNA, were performed using a C1000 Touch Thermal Cycler (BioRad). Initial denaturation of the DNA was at 94°C for 2 min, followed by 43 additional cycles of denaturation at 94°C for 30 s, a constant annealing temperature of 50°C for 30 sec and extension at 72°C for 45 s. A final extension step of 5 min at 72°C was added after the last cycle. PCR products (5 µl) were separated on a 1.8% agarose gel with 1 x TAE buffer, stained with 2.5 µl GelRed™ Nucleic Acid Gel stain (Biotium). After electrophoresis at 100 V for 45 min, the bands were visualised under ultraviolet light and the sexes of the WTSs identified. Sex = "unknown", where the sex could not be evaluated because no feathers were sampled for an individual.

2.2.4 GPS data processing

Analysis of GPS data were performed using R version 2.15.1 (R-Development Core Team 2012) and 3.3.1 (R-Development Core Team 2016) and ArcGIS 10.5.1® (ArcMap ™, ESRI 2016©). All erroneous GPS locations (i.e. points indicating unrealistic flight speeds) were filtered (‘*speedfilter*’ in the package *trip;* McConnell et al. 1992). GPS points were generally inconsistent in time with positional gaps within the tracks. To correct for this, the filtered data were processed using a continuous time-correlated random walk model to estimate the approximate movement parameters of the shearwaters (*crawl* package; Johnson et al. 2008). Locations from the predicted foraging tracks were interpolated to one minute intervals (c*rawl* package; Johnson et al. 2008) to calculate the average flight speeds, maximum distance from the colony (greatest distance reached at sea from the last known point on land), total path length (sum of distances between all the interpolated points), trip duration (time difference between the last point on land to the first point on land after a foraging trip at sea; *geosphere* package; Hijmans 2016) and total distance travelled per day (total path length/duration; km.d^{-1}). The flight bearing of each trip was calculated as the direction travelled between the colony to the furthest point (package *fossil*; Vavrek 2011).

The overlap index suggested by Fieberg and Kockanny (2005) was implemented (i.e. the utilization distribution overlap index; UDOI), using the ad hoc calculation for the smoothing parameter to estimate the percentage overlap. Percentage overlap of foraging areas between different breeding stages (incubation, early chick rearing and late chick rearing) within sexes as well as the overlap between long vs short trips within the different breeding stages, fixed kernel home-range utilization distributions (UD; Worton 1989) were calculated using the GPS locations for complete foraging trips. The UDOI equals 0 for two home ranges that do not overlap, and it equals 1 when both UDs are uniformly distributed and show 100% overlap (Fieberg and Kochanny 2005). When successive short trips were recorded for an individual, only the first trip was used to calculate the UD to avoid pseudo-replication. The active foraging, core foraging and the “hot-spot” areas were defined to be within the 90% (UD90 area), 50% (UD50 area) and 25% (UD25 area) probability density contours respectively (Lyver et al. 2011). Spatial analysis and estimations of the overlap indices were performed using the package *adehabitatHR* (Calenge 2006). Kernel density contours were plotted against bathymetry contours generated by data from General Bathymetric Charts of the Oceans (GEBCO; http://www.gebco.net).

2.2.5 Data analyses

Data analyses were performed using R version 3.3.1 (R-Development Core Team 2016) and ArcGIS 10.5.1® (ArcMap ™, ESRI 2016©). To test if the flight characteristics (i.e. maximum distance from colony, total path length, trip duration, average flight speed, flight bearing and distance travelled per day) were influenced by the predictor variables (i.e. breeding stage, sex), a suit of candidate mixed models were fitted. To determine whether maximum distance from colony, total path length and trip duration were influenced by sex within different breeding stages, generalised linear mixed models (GLMMs) with Gaussian distribution of error terms were used, using a log-link function (*'glmer'* in the package *lme4;* Bates et al. 2015). Only a few complete tracks were recorded for the S1 late chick-rearing stage, subsequently data were excluded when analysing distance and duration variables. Linear mixed-effects models (LMMs) fitted by restricted maximum likelihood (REML; *'lmer'* in the package *lme4;* Bates et al. 2015) were used to test the effect of the breeding stage (including S1 data) and sex on the average flight speed, flight bearing and distance travelled per day. To reduce biases associated with autocorrelation resulting from using multiple data points from the same birds, the "Bird ID" was added as a random effect for all models. Model selection was carried out using Akaike information criteria (AICc; '*dredge*' in the *MuMIn* package; Barton 2016) with the most parsimonious models (ΔAICc $\leq$ 2) included (Burnham and Anderson 2003). The significant effect of the predictor variables on the trip characteristics was tested using Wald chi-squared tests (*'Anova'* in the *car* package; Fox and Weisberg 2011).

2.3 Results

2.3.1 Instrument recovery and classification of foraging trips

Due to battery failure, only one complete and three near complete trips (where the birds were clearly heading back to the colony and tracks ended approximately 35 km from the colony) were recorded for the S1 late chick rearing stage, while sections from eight more tracks lasting 0.4 – 3.7 days were recorded. Data for incomplete tracks were used to calculate average flight speed and bearing and utilization distributions were calculated using only the complete and near complete tracks. For S2, 81 complete tracks from 34 individuals were recorded (incubation n = 18 individuals; failed incubation n = 1 individual; early chick rearing n = 15 individuals)

2.3.2 Foraging trip characteristics

Analysis of trip characteristics indicated considerable heterogeneity between breeding stages and sexes (Table 2.1). All models indicated that breeding stage and sex were important (ΔAICc ≤ 2) in influencing the maximum distance from the colony, total path length as well as the flight duration, with the breeding stage as the most important determinant (Table 2.1). There was considerable variation in trip characteristics between males and females during the same breeding stages (Table 2.1 and 2.2). During incubation, shearwaters travelled further from the colony (incubation: 440.21 ± 366.93 km; early chick rearing: 94.40 ± 93.55 km; late chick rearing: 73.88 ± 17.87 km), over greater distances (incubation: 1503.15 ± 1290.97 km; early chick rearing: 321.60 ± 435.12 km; late chick rearing: 193.61 ± 24.27 km) and spent more time at sea (incubation: 10.68 ± 7.53 h; early chick rearing 1.89 ± 2.62 h; 0.84 ± 0.23 h) compared to early chick rearing as well as late chick rearing. The shearwaters also foraged over substantially larger areas during incubation than during chick rearing (Table 2.3).

The average distance travelled per day, flight speed and flight bearing from the colony were largely influenced by breeding stage and sex as well as the interaction between these factors. During incubation, both males and females flew towards the south-eastern side of Madagascar (between 21 - 27°S), approximately 241.70 ± 1.86° and 236.60 ± 41.30° from the colony respectively, where females flew further south of Madagascar than males (Fig. 2.2. A – B) in a direction WSW from the colony. During incubation, there was a high overlap between male and female active foraging areas (84.16 %) and their "hot-spot" and foraging areas also overlapped (i.e. 5.25 and 17.07 % respectively). During incubation, on average females flew slightly faster than males (19.59 ± 2.94 m.s^{-1} and 18.44 ± 3.12 m.s^{-1} respectively).

During early chick rearing, the flight bearing of individual tracked shearwaters leaving the colony heading towards potential foraging sites varied only slightly, and shearwaters generally travelled in an east-south easterly to north westerly direction from the colony. On average females flew more in a southerly direction than males (males and females flew towards 272.40 ± 46.51° and 236.60 ± 50.88° from the colony respectively). However, the percentage overlap between "hot-spot", core and active foraging areas (3.64, 7.89 and 32.32 % respectively; Fig. 2.2. C – D), were lower than that of the male and female shearwaters during incubation. Males flew slightly faster than females during the early chick rearing period (18.22 ± 3.14 m.s^{-1} and 17.17 ± 2.32 m.s^{-1} respectively). On average, adults travelled further per day during late chick rearing (217.15 ± 87.57 km. d^{-1}) than early chick rearing (175.83 ± 55.85 km.d^{-1}) and even less during incubation (126.43 ± 66.66 km.d^{-1}).

Table 2.1 The parameter estimates from the generalized linear mixed models (GLMMs) fitted to the foraging trip characteristics of Wedge-tailed Shearwaters breeding in Réunion Island. Models included sex (male and female) and breeding stage (incubation and chick rearing periods) as main effects as well as the interaction between the main effects. All models included the "Bird ID" as a random effect. The intercept, second-order Akaike Information Criterion (AICc) scores, change in AICc scores (ΔAICc), degrees of freedom (df) and logLik functions are indicated for each model. Black dots (●) and empty spaces indicate variables included and excluded from the models respectively, only models with ΔAICc score ≤ 2 are included.

	Intercept	Sex	Stage	Sex: Stage	df	logLik	AICc	ΔAICc	Weight
Duration	0.70		●		4	-131.73	272.1	0.00	0.54
	0.41	●	●		5	-131.07	273.1	1.02	0.33
Maximum distance	4.65		●		4	-392.73	794.1	0.00	0.52
	4.45	●	●		5	-392.45	795.9	1.77	0.22
Path Length	5.87		●		4	-469.27	947.2	0.00	0.41
	6.42				3	-470.74	947.9	0.69	0.29
	5.67	●	●		5	-469.09	949.2	1.99	0.15
Distance travelled per day	171.6	●	●	●	9	-437.01	894.5	0.00	1.00
Speed*	17.19	●	●	●	6	-157.28	328.0	0.00	0.49
	17.73		●		4	-160.41	329.5	1.49	0.23
Bearing*	237.50	●	●	●	6	-329.90	673.2	0.00	0.97

Table 2.2 Foraging trip characteristics, mean ± SD (range), of the male and female Wedge-tailed Shearwaters during incubation, early- and late-chick rearing on Réunion Island (season one and two). Where no sex is indicated, data includes grouped measurements from males, females as well as individuals that could not be sexed.

Breeding stage	Sex	Birds (trips)	Maximum distance (km)	Trip length (km)	Duration (d)	Distance travelled per day (km.d^{-1})	Bearing	Speed (km.h^{-1})
Incubation	All	18	440.21 ± 366.93	1503.15 ± 1290.97	10.69 ± 7.53	126.43 ± 66.66	242.40 ± 35.38	19.11 ± 2.82
		(21)	(36.27 - 1028.61)	(79.89 - 3433.25)	(0.93 - 21.15)	(12.03 - 237.19)	(174.00 - 301.40)	(14.09 - 24.74)
	Male	4	599.20 ± 384.39	1999.80 ± 1279.82	14.42 ± 4.02	125.80 ± 79.09	241.70 ± 1.86	18.44 ± 3.12
		(4)	(38.10 - 894.80)	(107.50 - 2928.60)	(8.93 - 18.59)	(12.03 - 191.29)	(239.70 - 244.10)	(14.09 - 21.47)
	Female	11	397.95 ± 380.29	1353.73 ± 1363.87	9.08 ± 8.35	132.95 ± 66.81	236.60 ± 41.30	19.59 ± 2.94
		(14)	(36.27 - 1028.61)	(79.89 - 3433.25)	(0.93 - 21.15)	(51.39 - 237.19)	(174.00 - 301.40)	(14.67 - 24.74)
Early chick rearing	All	11	94.40 ± 93.55	321.60 ± 435.12	1.88 ± 2.62	175.80 ± 55.85	252.70 ± 49.82	17.72 ± 2.77
		(54)	(22.34 - 465.59)	(88.30 - 2247.80)	(0.68 - 15.12)	(83.30 - 336.30)	(125.50 - 317.90)	(11.26 - 25.80)
	Male	6	113.32 ± 112.03	396.10 ± 551.70	2.22 ± 3.41	192.20 ± 64.40	272.40 ± 46.51	18.22 ± 3.14
		(24)	(22.34 - 465.59)	(88.30 - 2247.80)	(0.71 - 15.12)	(83.30 - 336.30)	(162.10 - 317.90)	(11.26 - 25.80)
	Female	4	88.56 ± 80.34	231.52 ± 340	1.71 ± 1.96	171.60 ± 45.52	236.60 ± 50.88	17.17 ± 2.33
		(24)	(32.22 - 341.45)	(89.69 - 1596.52)	(0.68 - 8.00)	(106.90 - 274.90)	(125.50 - 316.50)	(12.37 - 21.29)
Late chick rearing	All	4	73.88 ± 17.87	193.61 ± 24.57	0.84 ± 0.23	245.51 ± 74.96	235.91 ± 8.82	22.24 ± 2.75
		(4)	(52.37 - 89.91)	(157.86 - 213.69)	(0.65 - 1.11)	(169.74 - 312.69)	(229.43 - 248.82)	(18.40 - 24.31)
	Male	1(1)	66.06	213.69	1.11	192.51	234.06	22.1
	Female	3	76.49 ± 20.93	186.91 ± 25.22	0.74 ± 0.16	263.18 ± 80.97	236.52 ± 10.69	22.29 ± 3.64
		(3)	(52.37 - 89.91)	(157.86 - 203.25)	(0.65 - 0.93)	(169.74 - 312.69)	(229.43 - 248.82)	(18.40 - 24.15)

Table 2.3 ‘Hot-spot’, active and core foraging areas (indicated by the 25, 50 and 90% utilization distribution (UD) kernels respectively) of the male and female Wedge-tailed Shearwaters during incubation, early- and late- chick rearing on Réunion Island (season one and two). Where no sex is indicated, data includes grouped measurements from males, females as well as individuals that could not be sexed.

Breeding stage	Sex	25% UD area (km^2)	50% UD area (km^2)	90% UD area (km^2)
Incubation	All	1.17 x 10^5	6.10 x 10^5	27.98 x 10^5
	Male	1.24 x 10^5	5.52 x 10^5	21.40 x 10^5
	Female	1.78 x 10^5	6.66 x 10^5	27.55 x 10^5
Early chick rearing	All	0.19 x 10^5	0.88 x 10^5	6.38 x 10^5
	Male	0.93 x 10^5	2.53 x 10^5	8.40 x 10^5
	Female	0.53 x 10^5	1.58 x 10^5	5.04 x 10^5
Late chick rearing	All	0.06 x 10^5	0.16 x 10^5	0.46 x 10^5
	Male	0.02 x 10^5	0.05 x 10^5	0.21 x 10^5
	Female	0.05 x 10^5	0.14 x 10^5	0.44 x 10^5

2.3.3 At sea foraging distribution

During S1 and S2, the shearwaters foraged SE – NW of the breeding colony. The ‘hot-spot’, core and active foraging areas during incubation were substantially larger than during early chick rearing (incubation trips: 117 000, 610 000, 2 798 0000 km^2, chick rearing trips: 19 000, 88 000, 638 000 km^2 respectively; Table 2.3); where “hot-spot”, core and active foraging areas during incubation covered areas 6.16, 6.93 and 4.38 times larger than during early chick rearing. During incubation, one of the nests failed, however, the active foraging areas of the successful and failed nests still overlapped by 28.11% (Appendix Fig. B).

During incubation, the active foraging areas for the long trips were in a south westerly to westerly direction of the colony and shearwaters flew as far as the edge of the continental shelf of Madagascar in the East Madagascar Current (EMC) and surrounding open, deeper waters (2000 – 5500 m.b.s.l. Fig. 2.2. A). The males' active foraging areas were closer to the EMC; however, active foraging areas were 1.29 time smaller than the females', with their 'hot-spot' restricted to areas near the colony. Females flew further south to the Madagascar basin and the Madagascar Plateau (Fig. 2.2. A) and 'hot-spots' extended in deep waters (4000 – 4500 m.b.s.l.) approximately 165, 355 and 600 km away from the island and overlapped with the males' "hot-spots" near the colony (Fig. 2.2. A; Table 2.1). Overlap of 'hot-spots' were low (UD25: 5.25%; Appendix Table B) and predominantly occurred where shearwaters were foraging in the deeper waters near the colony and are a result of "high-traffic" areas where many shearwaters leave and return to the colony (as indicated by relatively straight tracks heading away or towards the colony; Fig. 2.2. B). Male and female core foraging areas overlapped in deep waters east of the south of Madagascar (approximately 50°E; 21°S and 49 - 50°E; 23 –24°S; Fig. 2.2. A). Important core and 'hot-spot' foraging areas for males and females were in deep waters between 4000 – 5500 m (Fig. 2.2. A). Short foraging trips during incubation lasted between 0.93 – 2.48 days and were very close to the island (110 ± 132 km; 100 – 3500 m.b.s.l.; Appendix Fig. C), covering a small active foraging area (2000 km^2; Appendix Table A).

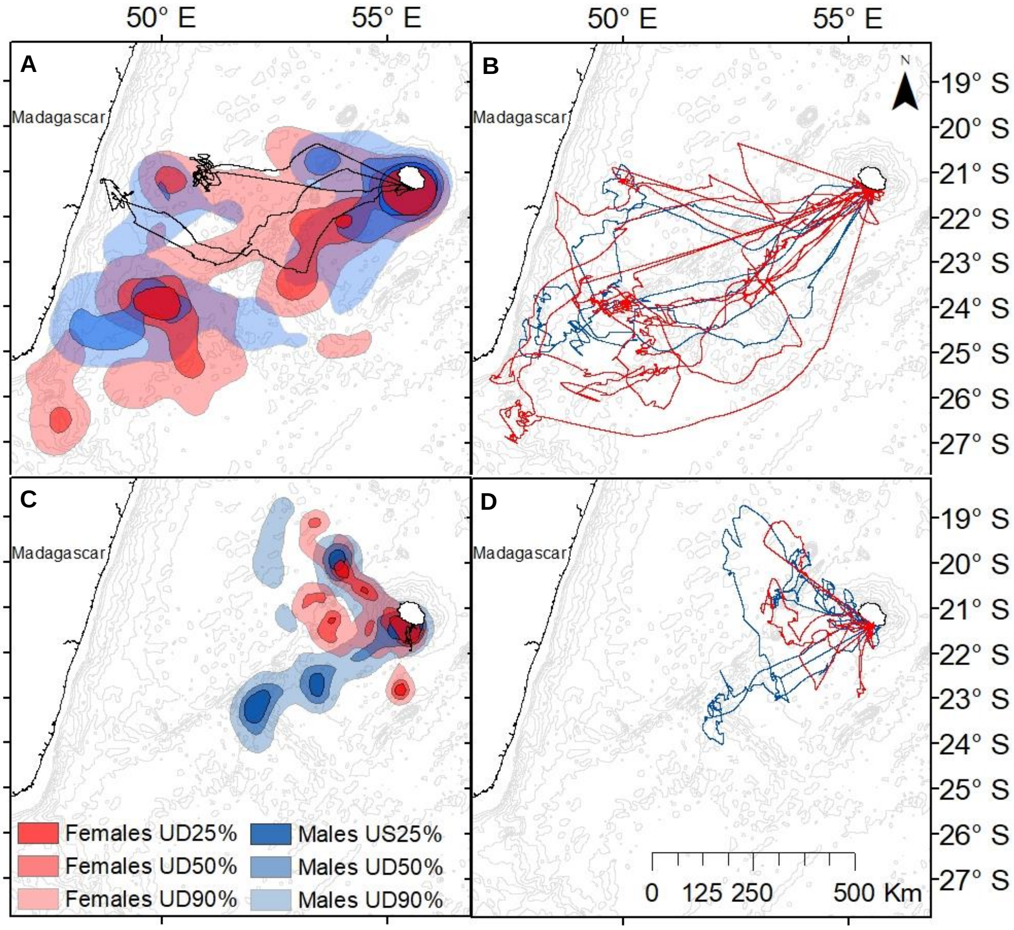


Figure 2.2 The “hot-spot”, core and active foraging areas (25, 50, 90% utilization distribution (UD) contours) for female (from darkest to lightest red respectively) and male (from darkest to lightest blue respectively) Wedge-tailed Shearwaters during **A.** incubation and **C.** early chick rearing at Grand Anse, Réunion Island. Individual foraging tracks where sex was not determined are in black. Single tracks from individual male (blue) and female (red) shearwaters during **B.** incubation (GPS tracks n = 18; males n = 4; females n = 11; unknown n = 3) and **D.** early chick rearing (GPS tracks n = 15; males n = 8; females n = 6; unknown n = 1)**.** Isobaths (light grey lines) are at 500m intervals between Réunion Island and Madagascar.

During early chick rearing, for male long trips, ‘hot-spot’, core and active foraging areas were 1.69, 1.75 and 1.94 times larger respectively than the female foraging areas, however, they were 2.75, 1.76 and 1.57 time smaller respectively than female foraging areas during short trips (Appendix Fig D). For long trips, during early chick rearing, active foraging areas for males and females extended eastwards into the Mascarene Basin and "hot-spots" overlapped near the Pérouse Seamount and surrounding waters near the colony (Fig. 2.2. C). Males extended their range further along the Wishaw Ridge north-west of the colony. The depth of "hot-spots" ranged between 500 – 5500 m.b.s.l., with shallower "hot-spots" forming near seamounts or areas surrounding Réunion Island. During short trips, the shearwaters remained near island SEE – SWS of the colony. The "hot-spot" areas did not extend past the 2500 m isobath; however, active foraging areas were over deeper waters (up to 4000 m.b.s.l.; Fig. 2.2. C). Female core foraging areas further extended further than the males' (Table 2.2), towards the Bourdonnais Ridge, near the Mauritius trench (Fig. 2.2. C and D). Though there were no differences in flight duration, maximum distance from colony and path length between males and females for long or short trips, the percentage overlap of "hot-spot", core and active foraging areas between the sexes for long (0.62, 2.08, 13.92 %) and short (2.43, 9.73, 46.23 %) trips were relatively low, indicating spatial segregation between the sexes.

2.3.4 Dual foraging

During chick rearing, it was visually evident that shearwaters implemented a dual foraging strategy (e.g. Fig. 2.3 a - e). Shearwaters would make several short trips near the island (< 3 days) before executing a single long trip (> 3 days). There were no consecutive long trips recorded. For all long trips, shearwaters flew beyond the 4000 m isobath. Long trips were significantly further (long: 262.26 ± 139.84 km, short: 69.40 ± 51.06 km; df = 1, $X^2 = 49.66$, $p < 0.001$) from the colony, and subsequently longer (long: 7.61 ± 3.96 d, short: 1.02 ± 0.36 d; df = 1, $X^2 = 147.89$, $p < 0.001$) on average, than short trips during chick rearing. The long and short trips did not seem to be well coordinated between parents, with several chicks being fed by both parents on one night, and then fasted for 2 – 6 consecutive nights where they lost between 9 – 77% of their body mass (*unpublished data* DZK).

2.3.5 Mass change after long trips and short trip cycles

On average, adults were significantly heavier by approximately 20 – 90 g at the end of a long trip (406.5 ± 29.5 g; incubation n = 12 and early chick rearing n = 1) than at the beginning (344.6 ± 17.5; incubation n = 12 and early chick rearing n = 1) of the same long trip (paired *t*-test: t = -11.50; df = 12, p < 0.001). There was a positive relationship between the mass gained during long trips and the duration of the same long trip (y = 26.91 + 2.53 x; adjusted $r^2 = 0.40$; $F_{1,11} = 7.43$; p = 0.02; Appendix Fig. E).

The number of short trips within a short trip cycle (number of consecutive short trips between two long trips) ranged between 2 – 9 trips. The mass of the adults prior to the first trip of a short trip cycle (i.e. before several trips to the nest) ranged between 335 – 430 g (388.3 ± 36.3 g, chick rearing n = 6) and this was not significantly greater when recaptured (before going on a long trip) ~370 – 418 g (389.7 ± 19.1 g, chick rearing n = 6) after several trips made by the same individual (paired *t*-test: t = 1.19; df = 4; p = 0.30). Though there was a negative relationship between mass loss and the number of trips made in a short trip cycle, it was not significant (y = 65.18 – 11.41 x; adjusted $r^2 = 0.37$; $F_{1,3} = 3.31$; p = 0.17). There was, however, a significant difference between the daily mass change during long trips where adults gained ~5 g d^{-1} (4.7 ± 1.7 g d^{-1}; incubation n = 12 and early chick rearing n = 1) and lost ~ 2 g d^{-1} (1.5 ± 2.9 g d^{-1}; chick rearing adults n = 6) during short trip cycles (student's *t*-test: t = 4.52; df = 5.13; p = 0.01).

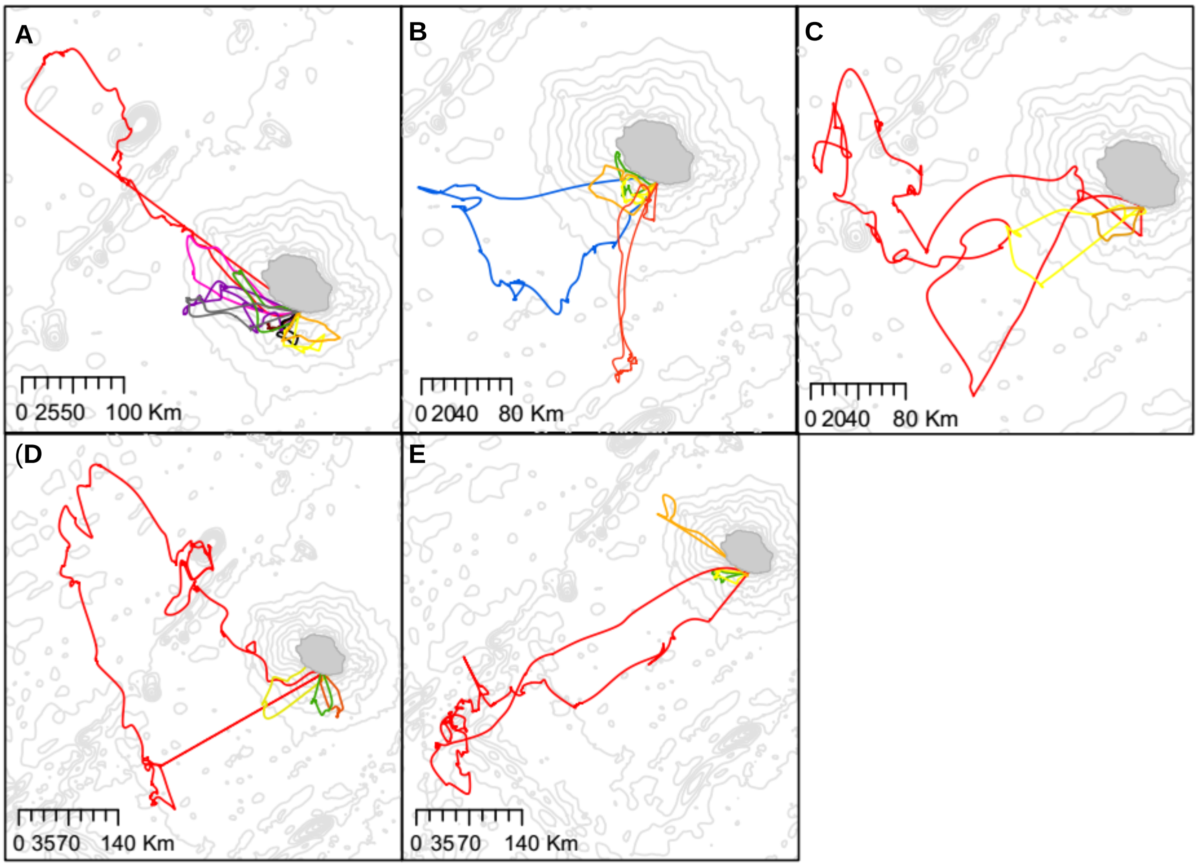


Figure 2.3 Tracks of a sample of Wedge-tailed Shearwaters indicating short and long foraging trips during the 2016/17 breeding season at Grand Anse, Réunion Island. During chick rearing the birds depart from the colony for several short trips before and/or after executing a single long trip (red or blue). **A.** Individual JAN2017_41 performed 8 short trips, followed by a single long trip (7.14 d). **B.** Individual JAN2017_64 performed 1 long trip (3.19 d), followed by 3 short trips and then 1 long trip (3.73 d). **C.** Individual JAN2017_71 performed 2 short trips followed by a long trip (8.00 d). **D.** Individual JAN2017_63 performed 3 short trips followed by a single long trip (15.12 d). **E.** individual JAN2017_59 performed 1 short trip followed by a single long trip (9.11 d) and then 2 short trips.

2.4 Discussion

This study is the first to look at the fine scale foraging distribution of Wedge-tailed Shearwaters breeding in the Indian Ocean, apart from a pilot study conducted by Cere et al. (2013), which included a limited number of trips (13), only during chick rearing. Shearwaters foraged over large areas within a relatively narrow range and utilized prominent oceanographic features (i.e. seamounts). I found that sexual segregation was more apparent during early chick rearing and during this time, shearwaters implemented a clear dual foraging strategy.

2.4.1 Influence of breeding stage and sex on the foraging ecology of Wedge-tailed shearwaters

As expected, during incubation, both male and female shearwaters spent significantly more time at sea and foraged further than during chick rearing. This is consistent with results from other central place foragers (Fernández et al. 2001; Phillips et al. 2006; Pinet et al. 2012). There was a high degree of spatial overlap between males and females during incubation and spatial segregation between sexes mainly occurred where females extended their range further towards the Madagascar Plateau. The shearwaters foraged close to the East Madagascar current which is also an important foraging area for the endemic Barau’s petrel (Pinet et al. 2012). Moreover, they foraged in areas where annual summer phytoplankton blooms occur, along southeast Madagascar in the western Indian Ocean (Longhurst 2001; Srokosz et al. 2004; Raj et al. 2010; Oozeeraully 2015; Komul 2016). It is possible that the shearwaters synchronise their breeding periods with periods when primary productivity is higher, more predictable and localised, allowing them to meet the high energetic requirements of breeding. This pattern has been described for other seabird species in the tropical western Indian Ocean (Jaquemet et al. 2007; Pinet et al. 2012).

During incubation and early chick-rearing, the shearwaters utilized similar active and core foraging areas, especially areas close to Réunion Island. The ‘hot spots’ during both breeding stages were located near the colony and in small areas in the pelagic ocean between Réunion Island and Madagascar during incubation. During long foraging trips, throughout incubation and early chick rearing, shearwaters travelled great distances (mean maximum distance: 605.00 ± 333.71 km and 291.45 ± 159.88 km respectively) to replenish their body reserves. These distant sites must provide some advantage (e.g. potential energy gain) to overcome energy expenditure (Weimerskirch and Cherel 1998). Subsequently, these sites are potentially areas of high prey availability and/or reliability to maintain long-term reproductive success (McDuie et al. 2015).

Shearwaters showed greater sexual segregation during early chick rearing. Observed foraging locations during early chick rearing (as well as short trips near Réunion Island during the incubation period) are characterised by rapidly changing bathymetric gradients near seamounts that are surrounded by deep waters (Lénat 2016). Such sites, like seamounts, are notorious for their high biodiversity (Clark et al. 2010) and known to increase prey availability to upper trophic level predators such seabirds (Haney et al. 1996; Thompson 2008) and tuna (Holland et al. 1999). Though the area surrounding Réunion Island is considered less productive, such areas would allow the adult shearwaters to adequately provide for their chicks before or after self-provisioning.

Shearwaters showed substantial differences between sexes in foraging trip characteristics. Despite being monomorphic and utilizing similar spatial habitats during the incubation period, females foraged over a larger area and on average travelled further per day compared to males. The larger spatial area utilized by the females may have been a result of variation between individual females or increased searching effort to locate specific food sources. Sex-specific differences in seabird foraging trip characteristics could be due to different reproductive roles or different energetic or nutritional requirements (Lewis et al. 2002; Phillips et al. 2006; Elliott et al. 2010). For example, it is possible that females prey on species with a greater nutritional content to make up for egg production (Nisbet 1997; Lewis et al. 2002). Egg production in seabirds is costly (Monaghan et al. 1998; Nager et al. 2001) and female shearwaters generally lay a single egg per clutch weighting approximately 60g (Ackerman et al. 1980). This is approximately 16% of their body mass and this investment is expected to necessitate relatively high foraging effort.

In contrast to previous studies for seabirds during chick rearing (Lewis et al. 2002; Peck and Congdon 2006; Thaxter et al. 2009; Elliott et al. 2010; Pinet et al. 2012), on average females foraged closer to the colony, over a smaller area (for long trips), and spent less time foraging than males. Females also did not spend more time foraging during long trips than males, thus there was no indication of greater allocation of females towards self-maintenance. Since active flight is a costly form of locomotion (Norberg 1996), by minimising the time spent flying or actively foraging, the females may expend less energy. Females may adopt different foraging strategies during the pre-laying exodus or during the late chick rearing period to make up for nutritional and or energetic requirements (Catry et al. 2009b). Unfortunately, no full tracks were retrieved during this period.

The foraging distribution is largely consistent with findings from previous studies in the tropical western Indian Ocean. Based on visual observations and data from geolocators, shearwaters have been shown to typically forage over relatively deep waters (Catry et al 2009b), in the open ocean and/or on the south – south-west of Réunion Island nearing 28°S, near Madagascar (Bailey 1968; Stahl and Bartle 1991; Jaquemet et al. 2004; Le Corre et al. 2012). Their continuous use of foraging areas in the south – south-west of the breeding colony may be to avoid competition from breeding Wedge-tailed Shearwaters from Round Island, Mauritius, which is home to the largest population (33.9%) of shearwaters in the Western Indian Ocean (MWF & NPCSM 2008 in Kappes et al. 2013) approximately 280 km away.

2.4.2 Dual foraging strategy

The study confirmed that shearwaters from Réunion Island implemented a dual-foraging strategy during chick rearing, similar to other populations in the tropics (Congdon et al. 2005; McDuie et al. 2015). This strategy is likely associated with building up of body reserves during long-trips, after not being able to self-provision adequately during short-trip cycles while attempting to meet the high energetic demands of the fast-growing chicks (Weimerskirch et al. 1994; McDuie et al. 2015).

During the 2016/17 early chick rearing period, adult shearwaters from Réunion Island there was a clear dichotomy between short-trip cycles (i.e. several short-trips lasting ≤ 2.54) near the island and single long-trips (> 3 to 15 d) where the shearwaters foraged in distant, deeper offshore waters. These distances and durations were comparable with other tropical shearwater populations breeding in Heron Island in the Southern Great Barrier Reef (Congdon et al. 2005; McDuie et al. 2015).

Shearwaters gained significantly more weight after a long trip during chick rearing, suggesting that these trips are implemented for self-maintenance where they replenished their body reserves after short trip cycles (Weimerskirch et al. 1994; McDuie et al. 2015). Short trips allow them to increase the frequency at which the adults can feed the chicks, at the cost of their own body condition (Weimerskirch et al. 1994). The high abundance of Wedge-tailed Shearwaters foraging between the 500 m and 1000 m isobaths near Réunion Island observed by Jaquemet et al. (2004), are likely those employing short foraging trips. Though mass change for only a few short trip cycles were recorded, during short trips, the shearwaters did not always lose weight and their body mass varied considerably (mass change range: - 40 to + 55 g). Individuals whose tags were left on for a greater number of consecutive short trips experienced greater weight loss while making multiple short trips to satisfy the chicks’ requirements before reaching a ‘critical’ mass and leaving on a long trip bout (Weimerskirch and Cherel 1998).

During incubation, though the shearwaters performed both long and short trips (Appendix Fig. C), it should be noted that short trips occurred near the end of the incubation period, a few days before the chick hatched. Short trips during this period may have been initiated to ensure that the chick was fed soon after hatching.

2.4.3 Conclusion future and directions

This study confirmed the deep waters on the south-west of Réunion Island as important foraging areas for the Wedge-tailed Shearwaters as well as parts of the south western Indian Ocean near the EMC. It revealed the sex-specific foraging strategies in a monomorphic seabird, that are likely to be driven by variances in energetic or nutritional requirements between the sexes. Furthermore, the shearwaters do implement a dual foraging strategy during chick rearing. It would be interesting to determine whether the diet and/or sources differ for long vs. short trips.

Shearwaters consistently foraged SE – NW of the breeding colony and their foraging areas overlap with important foraging sites for other seabirds in the tropical western Indian Ocean as well as industrial fisheries which target tuna (Le Corre et al. 2012). This further highlights these areas as areas of conservation concern. Further research will need to be done on the shearwater population on Round Island to assess potential competitive interaction and foraging segregation between the two colonies. The foraging distribution observed for birds from Réunion could potentially be associated with competition avoidance with the much larger shearwaters colony at Round Island.

CHAPTER 3

COMPARATIVE FORAGING ECOLOGY OF WEDGE-TAILED SHEARWATERS (*ARDENNA PACIFICA*) BREEDING IN THE TROPICAL WESTERN INDIAN OCEAN

3.1 Introduction

Climate change is a major threat to biodiversity (Thomas et al. 2004) and has resulted in shifts in species abundance and distribution (Walther et al. 2002; Burrows et al. 2011). In marine ecosystems, abiotic and biotic factors largely influence prey availability and abundance, driving variability at various spatio-temporal scales (Hunt and Schneider 1987). These ecosystems have largely been influenced by climate change (see review by Grémillet and Bouliner (2009)). Predators in turn potentially respond to the abundance, distribution, mobility and predictability of their prey (Bell 1991) through adapting behaviourally to local contexts. To overcome variations in prey distributions, various animal taxa have been shown to demonstrate a great deal of plasticity in their foraging behaviour (Nussey et al. 2007). This is particularly essential for species that are long lived, since changes in their microevolutionary responses are likely to be too slow to respond to the current rate of ecosystem changes (Wingfield 2003).

Seabirds are particularly suitable in comparative studies aimed at understanding animal responses to varying environmental conditions. This is because they are widespread throughout the world’s oceans. They show slow population growth and individuals are long lived with high adult survivorship (Ricklefs 1990). Seabirds spend most of their lives foraging over the ocean, only coming to land to breed (Schreiber and Burger 2001). Most of these seabirds are synchronous breeders, breeding in large colonies on islands (Coulson 2001). There are many advantages to colonial breeding, such as antipredator strategies, stimulation of immature seabirds (Coulson 2001) and relaying of social information (Schreiber and Burger 2001; Danchin et al. 2004). However, breeding in such large numbers also has its drawbacks. As central place foragers, they often need to travel large distances in search of prey since food resources are not always available near the breeding colony (Coulson 2001) and are hypothesised to deplete quickly for large colonies of seabirds (Ashmole’s halo; Gaston et al. 2007). Furthermore, seabird colonies are often located close to one another, potentially resulting in resource partitioning between individuals form different colonies (Wakefield et al. 2013).

As a result of the life history traits of seabirds, they are particularly at risk to a wide range of impacts at sea, specifically climate change, human exploitation and pollution (González-Solís and Shaffer 2009; Croxall et al. 2012). This is particularly relevant considering our ever-increasing use of the oceans at industrial scales (Halpern et al. 2008) as well as climate change (Grémillet and Boulinier 2009).

Seabirds can commute hundreds of kilometres between their breeding colonies and their foraging grounds. With the advancement of tracking technology, a spatial component can be integrated when studying the interactions between seabirds and marine ecosystems (González-Solís and Shaffer 2009). Wedge-tailed Shearwaters *Ardenna pacifica* are one of the dominant species of seabirds breeding in the WIO, with a breeding population size of approximately 246 075 and 229 075 in Seychelles and Mascarenes respectively (Danckwerts et al. 2014). Intra-specific competition is expected to be high between conspecifics due to the lack of niche partitioning between similar species (Grémillet et al. 2004; Begon et al. 2006). This may explain why several species of seabirds demonstrate sexual segregation while foraging (Lewis et al. 2002; Catry et al. 2009b; Thaxter et al. 2009; Elliott et al. 2010; Pinet et al. 2012; Botha et al. 2017) to alleviate intra-specific competition.

Wedge-tailed Shearwaters mainly feed on fish prey and cephalopods (Catry et al. 2009a). However, like many other seabirds in the tropics, they have a near obligate relationship with subsurface marine predators, especially tuna, which they rely on to drive these prey species to the surface (Jaquemet et al. 2004). Thus, it is expected that their foraging distribution to a large extent will reflect that of these predators. I aimed to compare the foraging ecology of Wedge-tailed Shearwaters (hereafter shearwater) breeding in the tropical western Indian Ocean, namely: D'Arros Island (5°, 24'S; 53° 18' E) and Fouquet Island, St Joseph Atoll (5° 25'S; 53° 20' E) in Seychelles as well as Grand Anse, Réunion (21°37'S; 55°55'E; see Fig. 1.1).

Shearwaters have a seasonal breeding cycle (Whittow 1997) and birds from Seychelles start breeding in late September – October whereas the shearwaters from Réunion breed later in the year during late November – December. This temporal segregation of breeding periods allowed for this comparative study. Therefore, specifically, I aimed to (1) map the foraging distribution of Wedge-tailed Shearwaters tracked from three colonies during incubation and relate it to abiotic factors, (2) compare the flight characteristics of the three colonies and lastly, (3) assess the potential spatial segregation and/or overlap between neighbouring colonies.

3.2 Materials and Methods

3.2.1 Study area

3.2.1.1 D'Arros and Fouquet Island

Partly due to all the islands and atolls in Seychelles, it has a large economic exclusion zone (EEZ) of approximately 1 338 000 km^2 with a relatively small total landmass (445 km^2; Fig. 1.1 and Fig. 3.1). D'Arros and Fouquet Islands are part of Seychelles' outer coralline islands in the Amirates group. Between December and March, these islands are dominated by the northwest monsoon and then between April and November the southeast trade winds. The shearwaters' breeding season co-occur with two of the major phytoplankton blooms in Seychelles archipelago. The first occurs between May to August, and the second occurs between December to February (Monticelli et al. 2007; Catry et al. 2009b). There are an estimated 3 100 breeding pairs of shearwaters on D'Arros Island (*unpublished data* DZK) and 28 655 on Fouquet Island (Kappes et al. 2013).

D'Arros Island is a privately-owned retreat and research station which supports conservation efforts on D'Arros as well as St Joseph Atoll. D'Arros' 30 m isobath lies between 1 – 1.4 km from the reef edge with gradual reef slopes to the west and south of the island. The slope is very steep on the northern and eastern side of the island where the isobath lies 100-300 m from the reef edge. D'Arros and St Joseph Atoll are separated by a 1.1 km wide channel (60 – 70 m deep). Fouquet is part of the St Joseph Atoll which lies of the eastern edge of the Amaranths Bank. On the western side of the atoll, bottom depths do not exceed 50 m. However, on the eastern side, 1.5 km from the reef edge, bottom depth reaches up to 500 m (Stoddart et al. 1979).

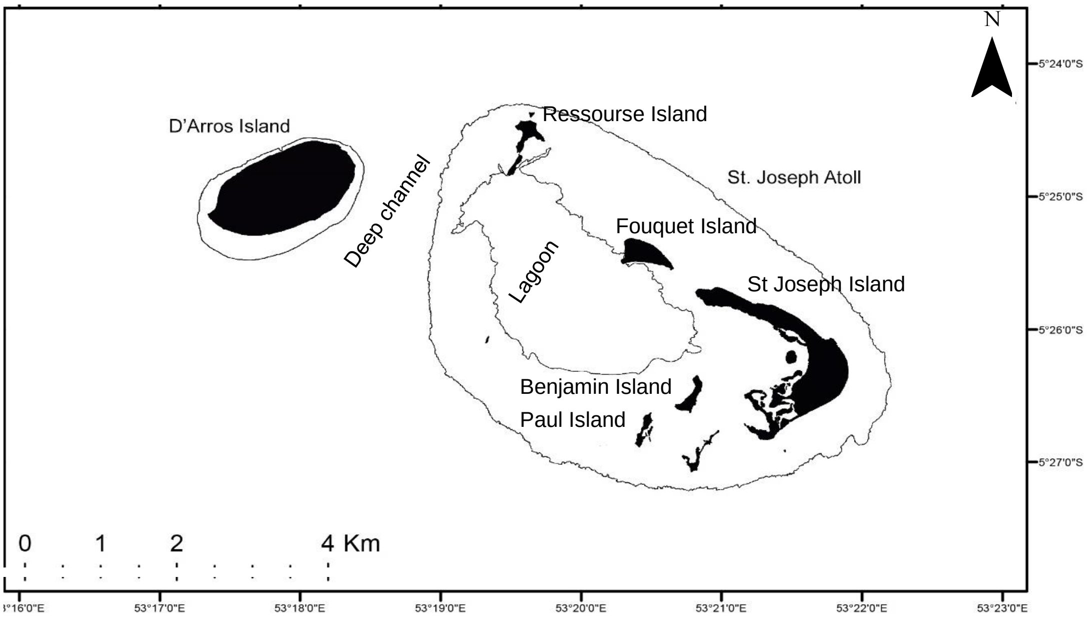


Figure 3.1 Map of D'Arros Island and neighbouring St Joseph Atoll, Seychelles.

3.2.1.2 Réunion Island

Réunion Island is a volcanic island lying on the westernmost end of the Mascarene Island group (Duncan and Hargraves, 1990). More than 60% of the island is 1 000 m above sea level and reefs and islets are almost absent around the coastline. It has an area around 2 512 km^2 and a surrounding EEZ of approximately 316 000 km^2 (Fig. 1.1). Tropical depressions and the south-east trade winds dominate the climate. A High rainfall, which co-occurs with the shearwater's breeding season, is brought by cyclones and the wettest, hottest months between December and April during the monsoon season (Le Corre and Safford 2001). Between 18.52 km and 55.56 km from the coast, isobaths reach 1 500 m and 3 500 m respectively (Le Corre and Safford 2001). The island is surrounded by homogeneous oceanic environment with no nearby upwelling areas (Jaquemet et al. 2004). There are approximately 900 breeding pairs of Wedge-tailed Shearwaters on Réunion (*unpublished data* MLC)

3.2.2 Data collection

Data were collected during the early incubation period from Seychelles and Réunion during September – October 2017 and December 2016 respectively. In Seychelles, 45 CatTraQ2™ GPS loggers (Catnip Technologies, USA; 44 mm x 23 mm x 12 mm, 12 g) were deployed on shearwaters, 21 on D'Arros Island and 24 on Fouquet Island and 35 CatTraQ2™ GPS loggers were deployed on Réunion Island. The loggers were covered in clear heat-shrink tubing for waterproofing and were attached to the shearwater's tail feathers using strips of TESA® tape (Beiersdorf AG, Germany). All loggers weighed ≤ 4.3 of the shearwaters' body mass (average bird mass before foraging trip = 346 ± 21 g). To identify the deployed bird in the burrow, birds were marked on their breast and head feathers with non-toxic white paint (Genuine Heritage Craft Products, South Africa).

Incubating shearwaters were carefully removed from their burrows and equipped with above-mentioned loggers. Relatively light birds (weighing < 380 g) were selected, since birds lose about 10 g/day on average while incubating (*unpublished data* DZK), and were likely to depart within a few days on a foraging trip (following partner changeover). To avoid unnecessarily draining of the batteries while the birds were in the burrow, the loggers were set to start recording after 2 – 4 days following deployment. The loggers were programmed to log position every 60 min. For molecular sexing purposes, on retrieval, breast feather samples were plucked and blood was collected using sterile syringes (BD Micro-Fine™ insulin syringes; 0.30 mm x 8 mm) washed with Sodium Heparin 5000 U.I./ml, leaving ~ 0.01 ml of Heparin in the syringe to prevent the blood from clotting. Average handling time was less than 8 min.

3.2.3 Molecular sexing

The 2550F (5’-GTT ACT GAT TCG TCT ACG AGA-3’) and 2718R (5’-TTG AAA TGA TCC AGT GCT TG-3’) primers were used to amplify fragments of the sex-linked CHD-1 gene (Fridolfsson and Ellegren 1999). These primers detect females as two fragments (ZW) and males as a single fragment (ZZ).

Shearwaters were molecularly sexed using blood or feather tips (described in Chapter 2). Not all birds were successfully sexed when using blood and subsequently, feather tips were used to sex the remainder of the birds. The DNeasy® Blood and Tissue Kit (QIAGEN®) was used to extract DNA from blood. Blood (5 – 10µl) was centrifuged at 190 rpm for 5 min. Blood samples were then re-suspended in 200 µl PBS and 4 µl proteinase K (1mg/ml) was added to the blood sample. Buffer AL (200 µl) was added to the blood mixture and thoroughly vortexed. The blood samples were then incubated overnight at 56°C. The following day, 200 µl of 96% ethanol was added to the blood samples and vortexed for 4 – 5 sec. The mixture was then pipetted into a DNeasy Mini spin column in a 2 ml collection tube and centrifuged at 8000 rpm for 1 min. The flow-through and collection tubes were then discarded and the spin column was placed in a new 2 ml collection tube. Buffer AW1 (500 µl) was added to the mixture which was then centrifuged at 8000 rpm for 1 min. The flow-through and collection tubes were discarded and the spin column was placed into another new 2 ml collection tube. Buffer AW2 (500 µl) was then added to the mixture which was then centrifuged at 14 000 rpm for 3 min. The flow-through and collection tubes were discarded and the spin column were transferred into a 1.5 ml microcentrifuge tube. DNA was eluted by adding 100 µl Buffer AE to the centre of the spin column membrane and samples were then incubated for 10 min at room temperature. Samples were then centrifuged at 8000 rpm for 1 min. To increase the DNA yield, the last step was repeated using 50 µl Buffer AE.

For the blood and feather samples, using a NanoDrop® 2000c Spectrophotometer (Thermo Scientific), 1µl of the extracted DNA mixture was used to measure the DNA yield. Polymerase chain reactions (PCR) in a 15 µl solution containing: 4.3 µl of molecular grade H_2O, 7.5 µl of GoTaq® G2 Hot Start Green Master Mix (Promega), 0.6 µl; 50 nmol of each primer and 40 – 410 ng (2 µl; 50 nmol) DNA, were performed using a C1000 Touch Thermal Cycler (BioRad). Initial denaturation of the DNA was at 94°C for 2 min, followed by 43 additional cycles of denaturation at 94°C for 30 s, a constant annealing temperature of 50°C for 30 sec and extension at 72°C for 45 s. A final extension step of 5 min at 72°C was added after the last cycle. PCR products (5 µl) were separated on a 1.8% agarose gel with 1 x TAE buffer, stained with 2.5 µl GelRed™ Nucleic Acid Gel stain (Biotium). After electrophoresis at 100 V for 45 min, the bands were visualised under ultraviolet light and the sexes of the birds identified. Sex for some birds were unknown, in the case where no feathers or blood were sampled for an individual.

3.2.4 GPS data processing

GPS data were processed using R version 2.15.1 (R-Development Core Team 2012) and 3.3.1 (R-Development Core Team 2016) and ArcGIS 10.5® (ArcMap ™, ESRI 2016©). All erroneous GPS locations were filtered (‘*speedfilter*’ in the package *trip;* McConnell et al. 1992). To process filtered data and further correct for positional gaps within the GPS tracks, a continuous-time correlated random walk model to estimate the approximate movement parameters of the shearwaters (*crawl* package; Johnson et al. 2008). The predicted foraging track locations were interpolated to one minute intervals (c*rawl* package; Johnson et al. 2008) to calculate the trip duration (time difference between the last point on land to the first point on land after a foraging trip at sea; *geosphere* package; Hijmans 2016), total path length (sum of distances between all the interpolated points), maximum distance from the colony (greatest distance reached at sea from the last known point on land), average flight speeds and the flight straightness index (beeline distance between the initial and final points of the flight divided by the total distance travelled in the flight; Batschelet 1981; Benhamou 2004). The flight bearing of each trip was calculated as the direction travelled between the colony to the furthest point (package *fossil*; Vavrek 2011).

Fixed kernel utilization distributions (UD; Worton 1989) were calculated using the GPS locations for foraging trips to determine the percentage overlap between different islands (i.e. D’Arros, Fouquet and Réunion) as well as between sexes from different islands. To estimate the percentage overlap between groups, the utilization distribution overlap index (UDOI) was calculated, using an ad hoc calculation suggested by Fieberg and Kochanny (2005) for the smoothing parameter. Probability density contours were used to identify the active foraging, core foraging and the “hot-spot” areas and were defined to be within the 90% (UD90 area), 50% (UD50 area) and 25% (UD25 area) ranges respectively (Lyver et al. 2011). When two home ranges perfectly overlap, the UDOI equals 1 (indicating 100 % overlap) and 0 when both UDs do not overlap (Fieberg and Kochanny 2005). Estimations of the overlap indices and spatial analysis were performed using the package *adehabitatHR* (Calenge 2006).

3.2.5 Data analysis

Data analyses were performed using R version 3.4.3 (R-Development Core Team 2016). Analysis of variance (ANOVA) was used to test for differences between trip duration, total path length, maximum distance from colony and average flight speed among the different islands and between sexes within the islands (‘*aov*’ in the *stats* package; Chambers et al. 1992). Kruskal-Wallis rank sum test was used to test for differences between flight bearing and flight straightness among the different islands and between sexes from the islands (*‘kruskal.test’* in the *stats* package; (Hollander and Wolfe 1973). A significance level of α = 0.05 was used, and results are presented as means ± standard deviation (SD).

Bathymetry data were generated from General Bathymetric Charts of the Oceans (GEBCO; http://www.gebco.net). Remote sensed Chlorophyll *a* data were downloaded from GlobColour (www.globcour.info) and SST data were downloaded from Oceans and Sea Ice Satellite and Application Facilities (OSI SAF; http://www.osi-saf.org).

3.3 Results

3.3.1 Instrument recovery

In Seychelles, three individuals lost their GPS loggers and several of the burrows were abandoned. In total, 15 loggers were retrieved from D’Arros (1 with no data) and 13 from Fouquet Island. In Réunion, 27 loggers were retrieved of which 15 had full tracks which were used for analysis.

3.3.2 Foraging trip characteristics

There were no significant differences in flight characteristics (i.e. flight duration, path length, maximum distance from colony, flight bearing and average flight speed and flight straightness) between sexes from any of the three islands with all comparisons yielding p values of less than 0.05 (Table 3.1). There were also no significant differences in flight straightness between sexes from the different islands (D’Arros: 6.30 $x10^{-5}$ ± $1.12x10^{-4}$, Fouquet: $2.10x10^{-5}$ ± $3.70x10^{-5}$ and Réunion: $4.71x10^{-4}$ ± $1.32x10^{-3}$; Kruskal-Wallis rank sum test: df = 5, X_2= 4.37, p = 0.50). The straightness index for most birds was very close to 0, indicating a general high sinuosity in the shearwaters’ flight paths.

For the following comparisons of these foraging metrics between sites, based on the above, data from the two sexes were accordingly lumped. The shearwaters from Réunion spent significantly more time at sea (15.35 ± 4.52 d; ANOVA: df = 2, F = 3.73, p = 0.03) than the shearwaters from Fouquet Island (11.99 ± 2.92 d; TukeyHSD: p = 0.05), but not from D’Arros (12.36 ± 3.11 d; TukeyHSD: p = 0.07). There was no significant difference in flight duration between D’Arros and Fouquet (TukeyHSD: p = 0.96; Fig. 3.2 A). There were no significant differences in total path length between D’Arros, Fouquet or Réunion Island (2171.50 ± 909.74 km, 1757.20 ± 482.25 km and 2254.10 ± 1041.65 km respectively; Kruskal-Wallis rank sum test: df = 2, X_2 = 5.18, p =0.08; Fig. 3.2 B). Shearwaters from Réunion flew significantly further from the colony than the shearwaters from Fouquet (610.80 ± 322.37 km and 393.60 ± 86.80 km respectively, Nemenyi-Tests: p = 0.03). However, there were no significant differences in maximum distance from the colony between D’Arros (535.00 ± 263.62 km) and Réunion or Fouquet and D’Arros (Nemenyi-Tests: p > 0.07; Fig. 3.2 C). The average flight speeds of the shearwaters from D’Arros (18.59 ± 2.79 $m.s^{-1}$), Fouquet (18.55 ± 1.88 $m.s^{-1}$) and Réunion (19.63 ± 2.81 $m.s^{-1}$) were very similar (ANOVA: df = 2, F = 1.75, p = 0.19; Fig. 3.2 D).

The individual shearwaters from D'Arros and Fouquet had a broad foraging range and flew towards a wide range of directions from their colonies (range: 44.44 - 329.39° and 51.54 - 325.33° respectively, Fig. 3.3 A and B). Shearwaters from Réunion had a more specific foraging range and mainly flew in a westerly to south-westerly direction of the colony (range: 223.00 - 277.00°, Fig. 3.3 B).

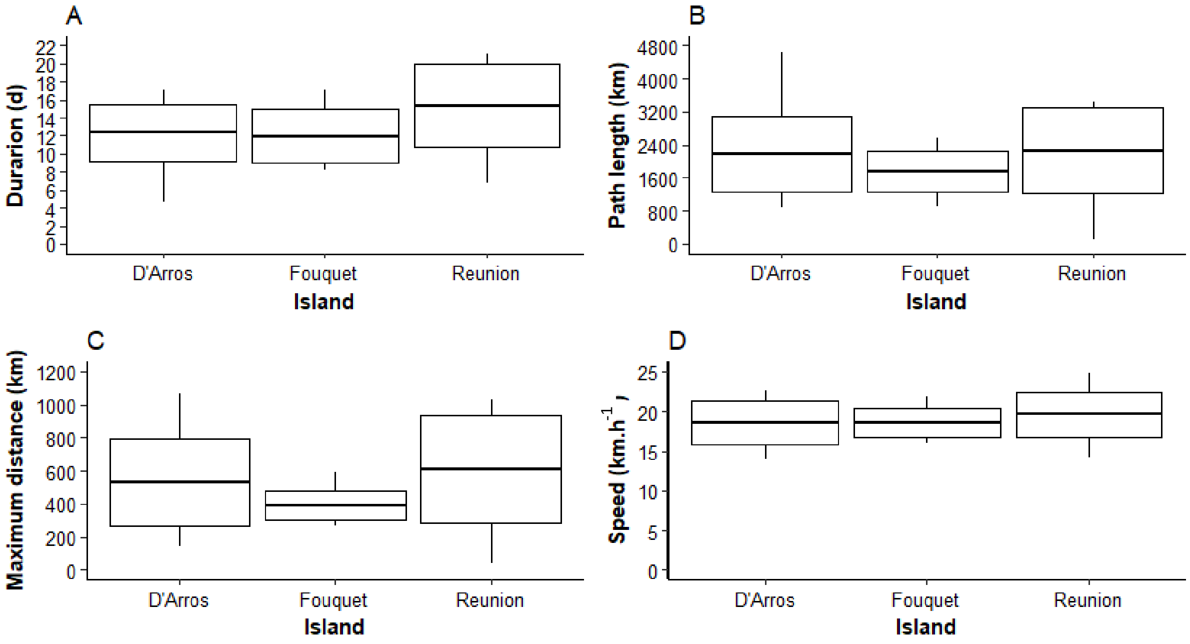


Figure 3.2 Boxplots representing the mean ± SD (min – max) of the trip characteristics (**A.** flight duration**, B.** total path length, **C.** maximum distance from the colony and **D.** average flight speed) for the Wedge-tailed Shearwaters from D'Arros, Fouquet and Réunion Island.

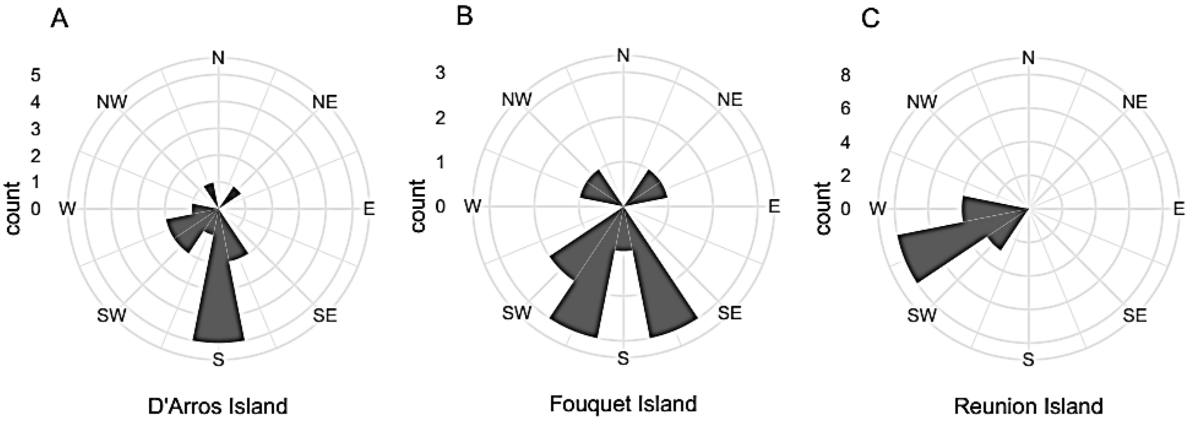


Figure 3.3 Frequencies of flight bearings (direction travelled between the colony to the furthest point) for Wedge-tailed Shearwaters from **A.** D'Arros, **B.** Fouquet and **C.** Réunion Island.

Table 3.1 The flight characteristics, mean ± SD (range) as well as the “hot-spot”, core and active foraging areas (UD25, UD50 and UD90 respectively) the of Wedge-tailed shearwaters from D’Arros, Fouquet and Réunion Island.

	n	Duration (d)	Path length (km)	Maximum distance (km)	Speed (km.h^{-1})	Bearing	UD25 (km^2)	UD50 (km^2)	UD90 (km^2)
D'Arros	15	12.36 ± 3.11 (4.74 - 17.06)	2171.50 ± 909.74 (882.70 - 4639.90)	535.00 ± 263.62 (141.70 - 1071.40)	18.59 ± 2.79 (13.92 - 22.57)	201.04 ± 65.19 (44.44 - 329.39)	35790	108020	393038
Male	8	12.07± 2.37 (7.97 - 15.17)	1882.00 ± 593.40 (1060.00 - 2758.00)	434.80 ± 212.48 (141.70 - 735.40)	19.96 ± 2.42 (15.05 - 21.63)	205.45 ± 88.64 (44.44 - 329.39)	20172	57951	244022
Female	4	11.99 ± 5.42 (4.74 - 17.06)	2500.70 ± 1563.98 (882.70 - 4639.90)	554.50 ± 359.37 (244.70 - 1071.40)	19.62 ± 2.60 (16.27 - 22.41)	203.30 ± 33.27 (173.30 - 234.40)	27330	78087	298032
Fouquet	13	11.99 ± 2.92 (8.14 - 17.14)	1757.20 ± 482.25 (916.20 - 2570.80)	393.60 ± 86.80 (271.70 - 590.20)	18.55 ± 1.88 (15.95 - 21.92)	189.44 ± 76.56 (51.54 - 325.33)	23426	76135	255750
Male	6	10.71 ± 3.46 (8.14 - 17.14)	1583.00 ± 575.35 (916.20 - 2481.00)	392.80 ± 66.53 (291.40 - 472.20)	18.70 ± 2.13 (16.29 - 21.92)	207.84 ± 93.71 (58.46 - 325.33)	26029	74183	231658
Female	7	13.08 ± 2.02 (9.87 - 15.00)	1907.00 ± 164.55 (1387.00 - 2571.00)	394.20 ± 106.67 (271.70 - 590.00)	18.42 ± 1.81 (15.95 - 21.52)	173.68 ± 61.46 (51.54 - 233.87)	18871	57915	196519
Réunion	15	15.35 ± 4.52 (6.78 - 21.15)	2254.10 ± 1041.65 (107.50 - 3433.20)	610.80 ± 322.37 (38.10 - 1028.6)	19.63 ± 2.81 (14.09 - 24.74)	247.00 ± 16.94 (223.00 - 277.00)	16268	70929	286319
Male	4	14.42 ± 4.02 (8.93 - 18.59)	1999.80 ± 1279.82 (107.50 - 2928.60)	599.20 ± 384.39 (38.10 - 894.80)	18.44 ± 3.12 (14.09 - 21.47)	241.70 ± 1.86 (239.70 - 244.10)	11062	49455	200423
Female	8	16.61 ± 4.57 (9.08 - 21.15)	2650.00 ± 783.35 (1212.00 - 3433.00)	686.14 ± 297.63 (54.68 - 1028.61)	20.93 ± 2.51 (16.90 - 24.74)	241.00 ± 16.62 (223.00 - 273.90)	25378	78738	279812

3.3.3 Utilization distribution and overlap at sea

The shearwaters from D'Arros Island (n = 15) utilised the largest "hot-spot", core and active foraging areas (UD25 = 3.58 x10^4 km^2, UD50 = 10.80 x10^4 km^2, UD90 = 39.30 x10^4 km^2). These foraging areas were 1.53, 1.42 and 1.54 times larger than Fouquet Island and 2.20, 1.52 and 1.37 times larger than foraging areas from Réunion respectively. The shearwaters' "hot-spot" and core foraging areas from Fouquet (n = 13) were slightly larger than Réunion's (n = 15), however, shearwaters from Réunion had larger active foraging areas (Fouquet: UD25 = 2.34 x10^4 km^2, UD50 = 7.61 x10^4 km^2, UD90 = 25.57 x10^4 km^2; Réunion: UD25 = 1.63 x10^4 km^2, UD50 = 7.09 x10^4 km^2, UD90 = 28.63 x10^4 km^2).

Despite broad foraging ranges observed for both D'Arros and Fouquet, the overlap between the "hot-spot", core and active foraging was limited (UD25% = 1.64 %, UD50% = 5.40 % and UD90% = 41.57 % respectively). There was no spatial overlap between foraging areas for the shearwaters from Seychelles and Réunion.

Despite small sample sizes, limiting an in-depth sex-specific comparison, there was also no clear evidence of sex-specific differences in foraging ranges (Fig. 3.4). Results indicated a low percentage overlap between males and females from D'Arros and Fouquet Island (UD90% = 20.52 % and 42.86 % respectively). Furthermore, no evidence of sexual segregation was evident when comparing the same sexes from different islands (combined male and female UD90% for male and female shearwaters were 25.09 % and 20.28 % respectively). The percentage overlap of the active foraging areas between the male and female shearwaters from Réunion Island, was particularly high (UD90% = 73.11 %).

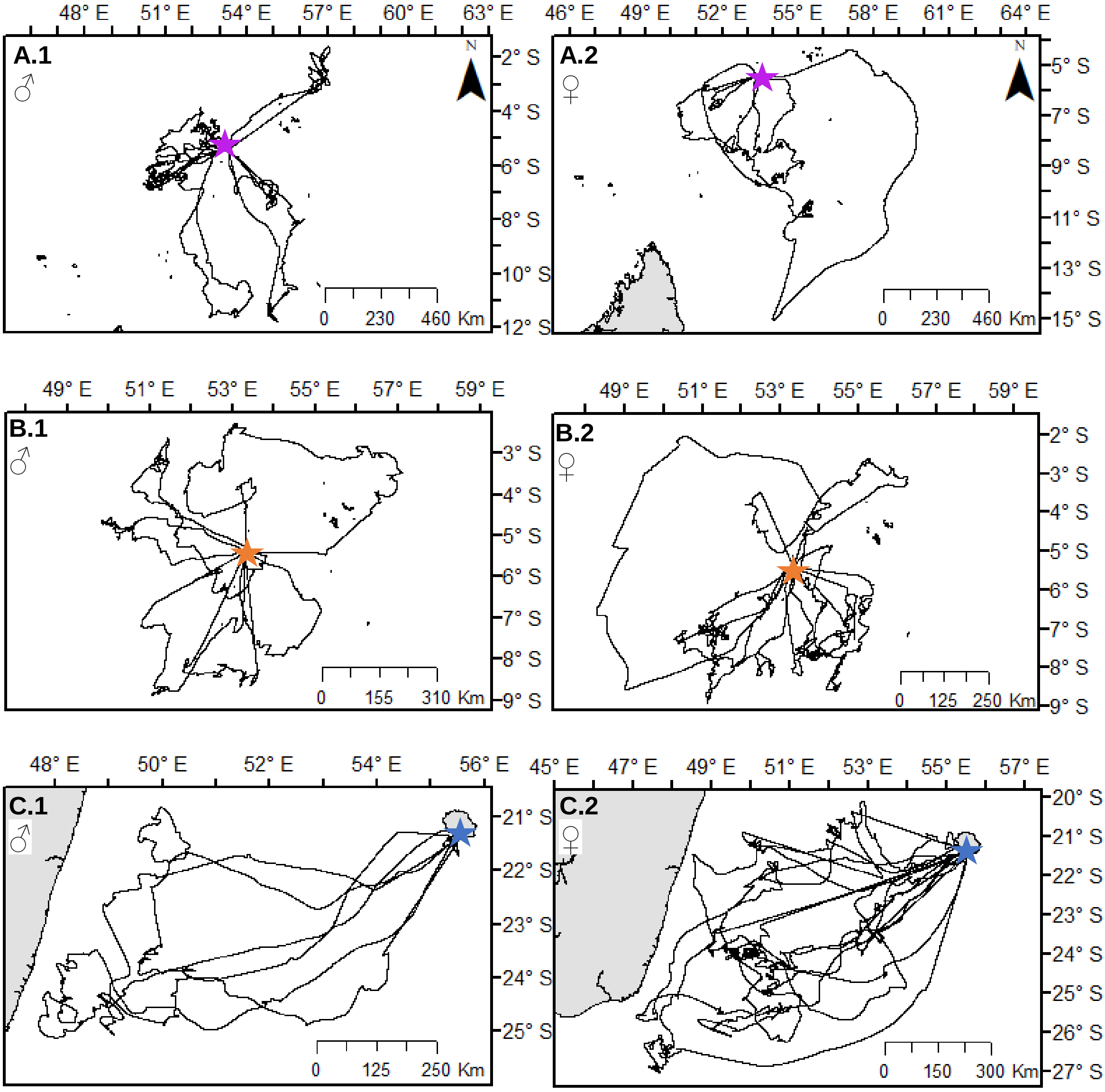


Figure 3.4 Single tracks of male (left) and female (right) Wedge-tailed Shearwaters from D’Arros Island (males: n = 8, **A.1**; females: n = 4, **A.2**), Fouquet Island (males: n = 6, **B.1**; females: n = 7, **B.2**) and Réunion Island (males: n = 4, **C.1**; females: n = 8, **C.2**). The purple, orange and blue stars indicate the location of the colonies for D’Arros, Fouquet and Réunion Island respectively.

3.3.4 Interaction with abiotic and biotic factors

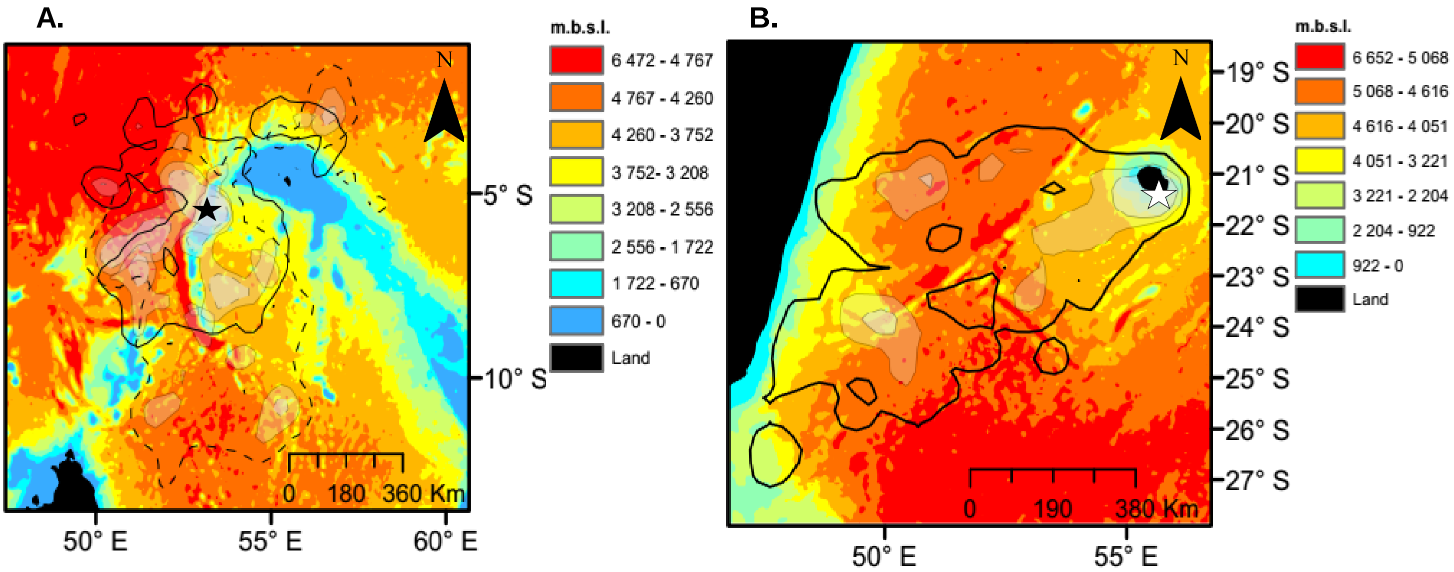


Figure 3.5 Contours of the active, core and 'hot-spot' foraging areas of Wedge-tailed Shearwaters foraging off **A.** D'Arros Island (dashed line) and Fouquet Island (solid line) as well as **B.** Réunion Island (solid line) are overlayed on bathymetry.

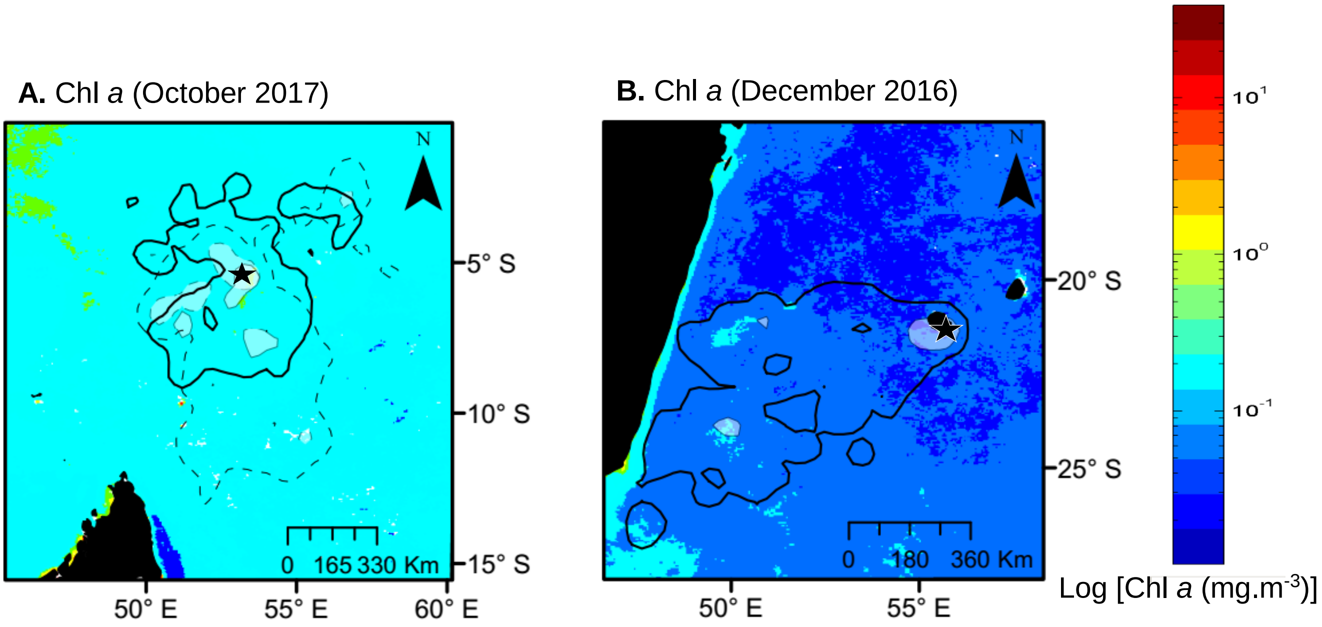
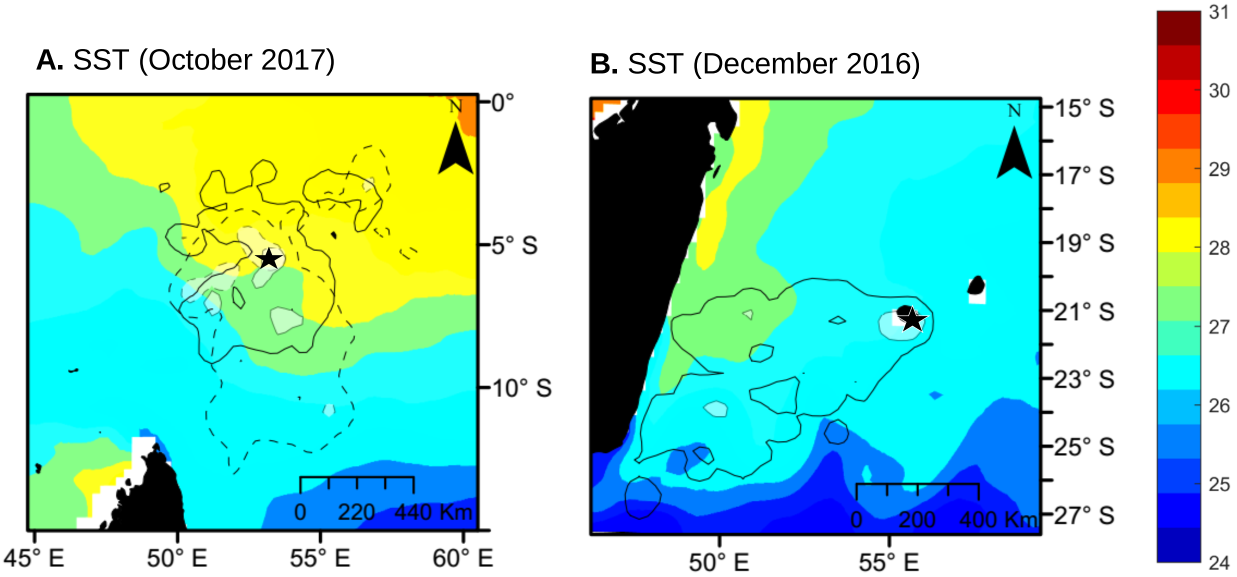


Figure 3.6 Remote sensed Chlorophyll *a* concentration (mg.m^{-3}) at the sea surface during the Wedge-tailed Shearwaters' incubation period for **A.** October 2017 and **B.** December 2016. Contours of the active foraging ranges of Wedge-tailed Shearwaters foraging off **A.** D'Arros Island (dashed line) and Fouquet Island (solid line) as well as **B.** Réunion Island (solid line) are shown.



A. SST (October 2017)

B. SST (December 2016)

Figure 3.7 Remote sensed sea surface temperature (SST; °C) during the Wedge-tailed Shearwaters incubation period for **A.** October 2017 and **B.** December 2016. Contours of the active and 'hot-spot' foraging ranges of Wedge-tailed Shearwaters foraging off **A.** D'Arros Island (dashed line) and Fouquet Island (solid line) as well as **B.** Réunion Island (solid line) are shown.

Bathymetry data indicate that shearwaters primarily forage over deep waters with the exception being near study colonies (Fig. 3.5). On average, active foraging areas for shearwaters from Seychelles were in areas of higher primary productivity than active foraging areas utilized by shearwaters from Réunion island. However, overall Chl *a* concentration was low (Fig. 3.6). Hot-spots for shearwaters from Seychelles overlapped near the Amirante Bank where primary productivity was relatively high. Hot-spots for shearwaters from Réunion Island were located near Madagascar, near areas of higher primary production. There was no apparent relationship with SST and shearwaters' active foraging areas or hot-spots, however, on average shearwaters from Seychelles foraged in warmer waters than Réunion (Fig. 3.7).

3.4 Discussion

3.4.1 Device effects

Not all loggers were retrieved as there were a number of nest failures. However, I do not expect that failures were caused due to handling stress, but rather natural causes. In Seychelles, it is presumed that some eggs may have been predated on by red hermit crabs *Coenobita perlatus* which was viewed in the 2016 breeding season by setting up camera traps (using GoPro Hero3) near burrows. Furthermore, some burrows had been abandoned after they collapsed (e.g. coconuts falling on the burrows and crushing them). It was also observed that during renovation of the burrows, shearwaters may not always be attentive of their eggs and have been seen kicking the egg to the front of the burrow and later retrieving it and moving deeper with their beak. This behaviour may cause eggs to break if they hit a hard substrate (personal observation DZK). Several birds, were seen at night near their burrows after eggs had disappeared and/burrows had collapsed, however, due to the high density of the nests, these loggers could not be retrieved and pursuing the birds may have proven destructive. In Réunion cats, rats and tenrecs were observed near nests, however, none were seen predating on the eggs; but see Faulquier et al. (2009).

3.4.2 Foraging distribution

The foraging distribution and flight characteristics of incubating shearwaters were derived from GPS data, collected from 43 individual birds from three different islands. During incubation, shearwaters from D'Arros and Fouquet utilised a wide range of ocean between 1°38' S to 13°03' S and 49°22' E to 58°25' E, covering active foraging areas of 393 038 km^2 and 255 750 km^2 respectively. Shearwaters from Réunion exploited a more restricted range between 20°00' S to 27°09' S and 47°12' E to 56°18 E encompassing an active foraging area of 286 319 km^2. Although seabirds are constrained to their colonies during the breeding periods, this study showed that shearwaters foraged long distances away from the colony, extending trips up to 1071 km, 590 km and 1029 km from D’Arros, Fouquet and Réunion respectively. These trips lasted up to 17 days for shearwaters from Seychelles and 21 days for shearwaters from Réunion. Interestingly, the average flight speeds of shearwaters across this this range did not differ.

3.4.3 Behavioural plasticity

Variability in foraging behaviour (i.e. foraging plasticity) at sea was illustrated in the different flight characteristics of shearwaters from different colonies. Foraging plasticity was mainly observed in the shearwaters’ flight bearing, flight duration and the maximum distance travelled from the colony. Shearwaters displayed dissimilar levels of site fidelity, where shearwaters from Réunion faithfully foraged towards SE Madagascar, while shearwaters from Seychelles foraged over a wide range over the Seychelles Basin. Foraging effort between shearwaters from Fouquet and Réunion was also significantly lower and shearwaters from Fouquet spent less time at sea and foraged closer to their colony. These difference in behaviour responses between colonies may be advantageous to shearwaters, indicating that they may be able to respond to some level of future environmental variability resulting from climate change and other anthropogenic pressures.

3.4.4 Interaction between colonies as well as with abiotic and biotic factors

To mitigate intra-specific competition, individuals from larger colonies are expected to travel further and spend more time at sea than smaller colonies (Lewis et al. 2001). This behaviour, however, was not evident between the two neighbouring colonies, D’Arros and Fouquet Island. Though the population of Wedge-tailed Shearwaters breeding on Fouquet Island is almost ten time larger than D’Arros Island, there were no significant differences in the flight characteristics between shearwaters from these islands. In this relatively homogenous environment where there are no clear indications of higher productivity and subsequently prey availability, separate colonies may act as sub-colonies of an individual breeding site (Ainley et al. 1995). D'Arros Island and Fouquet Island are separated by a narrow channel and are less than 4 km apart (Fig. 3.1). The shearwaters can easily cover this distance over a short period of time. According to Ainley et al. (1995), under such conditions, foraging zones should widely overlap and birds from different colonies should exhibit similar foraging effort. The shearwaters' breeding season in Seychelles coincides with enhanced ocean productivity around the archipelago (Monticelli et al. 2007) which may largely influence their foraging distribution (Catry et al. 2009b). Foraging opportunities for the shearwaters from the separate islands are likely to be similar and shearwaters from different colonies did not travel towards separate directions, but rather foraged over a range of foraging directions from the colony, explaining the 42 % overlap of active foraging areas between colonies. Since such a small proportion of the shearwaters' population in Seychelles was tracked, it is likely that interaction between individuals from these colonies are higher than estimated and that shearwaters have possibly developed unique foraging strategies to avoid competition with other seabirds breeding and roosting on these island during this period. Unlike studies on Cape Gannets *Morus capensis* (Grémillet et al. 2004) and Northern Gannets *Morus bassanus* (Wakefield et al. 2013) that have shown spatial segregation between neighbouring colonies, the distance between colonies and prey availability is likely to influence the extent of spatial segregation between species (Waggitt et al. 2014). However, this is not always the case and studies have found several species of penguins and the Imperial Shag *Phalacrocorax albiventer* (Masello et al. 2010) as well as the Cory's Shearwater *Calonectris borealis* (Ceia et al. 2015) from colonies only 2 km apart to show spatial segregation in foraging distributions.

In comparison to Seychelles, the area surrounding Réunion Island has markedly lower Chl *a* concentration during the shearwaters' incubation period and shearwaters consistently travel long distances over a narrow range toward Madagascar's shelf edge to forage. Similar to Pinet et al. (2012), spatial segregation between sexes during incubation was low (overlap of active foraging area was 73 %). This area (as described in Chapter 2) is associated with a persistent seasonal phytoplankton bloom which starts during the shearwaters incubation period and moves eastwards (Longhurst 2001; Srokosz et al. 2004; Raj et al. 2010). It is likely that the shearwaters gather towards this area as a predictable food resource and since the bloom is likely to aggregate zooplankton, which are preyed on by larger predatory fish and squid (Piontkovski and Williams 1995), it directly and/or indirectly supplies the shearwaters with food. This high productivity within the tropics, however, is not typical to tropical systems which are usually characterised by low productivity (Weimerskirch 2007). Thus, shearwaters from Réunion may rely on localised areas of higher productivity at distance from the breeding colony in order to gain enough energy before returning to the nests and fasting for an average of 15.35 ± 4.52 days. Shearwaters may avoid foraging further south either due to physical constraints or to avoid competition with Réunion's endemic Barau's petrel *Pterodroma baraui* (Pinet et al. 2012).

Previous studies using GLS loggers in Seychelles and Réunion showed that Wedge-tailed Shearwaters utilized similar areas (Catry et al. 2009b; Le Corre et al. 2012) to this current study. Shearwaters from D'Arros and Fouquet overlapped their foraging home range with shearwaters from Aride during the pre-breeding period (Catry et al. 2009b). However, unlike Catry et al. (2009b), shearwaters did not forage towards one direction and sexual segregation was not evident. Shearwaters from D'Arros and Fouquet foraged over a broad range of foraging directions. In this study, shearwaters exploited the Amirante Basin as well as the East Somali Basin, bordering the shallower section of Seychelle's archipelago. Shearwaters from D'Arros flew further east and foraged in 'shallower' waters (between 675 – 2556 m.b.s.l.) near the Mascarene Plateau. They also flew further south towards the north-east Madagascar and extended their home range into the Mascarene Basin. As previously discussed in Chapter 2, shearwaters from Réunion foraged south-east of Madagascar over a narrower foraging range. Overall, shearwaters foraged in deep waters, usually at least 3000 meters and in areas of low productivity. Though this behaviour is consistent with other studies (Catry et al. 2009b), it should be noted that this may be a result of habitat availability and not necessarily of habitat preference as the waters surrounding both Seychelles and Réunion are characteristically deep and generally have low primary production. However, it has been well documented that tropical seabirds associate with marine subsurface predators (Au and Pitman 1986; Au and Pitman 1988; Jaquemet et al. 2004). Previous studies have indicated that the foraging distribution of shearwaters overlap with yellowfin and skipjack tuna distribution (Catry et al. 2009b), which associate with changes in sea surface temperature (SST; Lehodey et al. 1997; Lu et al. 2001). Seasonal variation in SST indicate that temperatures rise nearing the shearwaters breeding season. Shearwaters from D’Arros, Fouquet and Réunion Island foraged in warm waters between approximately 26.5 – 28.0°C, 27.5 – 28.0°C and 24.0 – 27.5°C respectively. Similar to tuna distributions, here we found that shearwaters forage in warm, unproductive waters (Lehodey et al. 1997).

The shearwater’s foraging distribution overlapped with several potential threats, such as purse sein and long line fleets as well as areas at risk of maritime trade pollution (Le Corre et al. 2012). These foraging areas have been described as areas of medium to medium high human impact (Halpern et al. 2008). Furthermore, the foraging ranges of shearwaters (current study) overlap with areas of high seabird density (Le Corre et al. 2012) highlighting the importance of these areas for conservation management. Though the home ranges of the shearwaters from Seychelles mainly remained within Seychelle’s EEZ, some individuals from D’Arros Island extended their range into Madagascar’s and Mauritius’s EEZ. Some from Fouquet foraged beyond territorial waters into international waters. Shearwaters from Réunion largely extended their home ranges during incubation into Madagascar’s EEZ (see Fig 1.1 in Chapter 1). This suggests that if conservation measures should be put in place for seabirds like Wedge-tailed Shearwaters, it will require efforts not only from the countries these birds breed in, but surrounding countries will need to aid in conservation management.

CHAPTER 4

REPEATED FORAGING AREAS AND INCONSISTANT BEHAVIOURS BETWEEN INDIVIDUAL WEDGE-TAILED SHEARWATERS (*ARDENNA PACIFICA*)

4.1 Introduction

Predators respond to the abundance, distribution and predictability of prey, which largely influences how and where they forage (Bell 1991). Foraging efficiency is expected to increase when individuals learn where prey may be found over different spatial and temporal scales (Cairns and Schneider 1990; Hamer et al. 2001; Weimerskirch 2007). Individuals of some species have accordingly been found to develop familiarity with sites, thus enabling effective movement and foraging (Piper 2011; Meier et al. 2015; Wakefield et al. 2015). Seabirds in particular, sometimes show individual preferences to foraging sites (Coleman et al. 2005; Baylis et al. 2015), indicating that they can remember potentially profitable sites and/or oceanographic features (Schneider 1993; Wakefield et al. 2015). This behaviour tends to occur when resources are associated with predictable oceanic features, like seamounts (Haney et al. 1996; Thompson 2008; Clark et al. 2010) or annual phytoplankton blooms (Pinet et al. 2012). These predators predictably return to the same areas, rendering these areas important for conservation management (Piper 2011; Baylis et al. 2015).

Tropical marine ecosystems, however, are known to be of relatively low productivity in comparison to higher latitudes (Ashmole 1971; Au and Pitman 1986; Au and Pitman 1988). As a result, tropical seabirds have had to evolve energy efficient (Ballance and Pitman 1999) and flexible foraging strategies (Weimerskirch et al. 2005b). Like other seabirds, during the breeding season adults of tropical species are constrained to feed in areas near their breeding grounds to meet the energetic demands of their chicks as well as their own. Thus, locating prey in an optimal manner becomes essential for their own success as well as their chicks.

Individuals are faced with a trade-off: to forage in patches that are familiar (high site fidelity) or to continuously search for the most profitable areas, thus avoiding potentially less profitable patches. Tropical seabirds furthermore associate with tuna and other marine top predators (Au and Pitman 1986; Au and Pitman 1988; Jaquemet et al. 2004; Anderson 2014). Thus, it is expected that their distribution should reflect that of these subsurface predators (Au and Pitman 1986; Ballance and Pitman 1999; Jaquemet et al. 2004). Though tuna have been found to travel vast distances (Chen et al. 2005), they aggregate near oceanographic features, such as seamount (Worm et al. 2003; Morato et al. 2010) as well as fish aggregating devices (FAD; Jaquemet et al. 2004; Fonteneau et al. 2013).

Wedge-tailed Shearwaters are Indo-Pacific tropical seabirds with a wide distribution, spanning between 35°N – 35°S and 42°E – 104°W (BirdLife International 2016). Generally, their breeding cycle is seasonal and tends to be more synchronous in the tropics (Whittow 1997) and they show high nest site fidelity (Catry et al. 2009b). My aim in this chapter was to investigate the foraging behaviour of Wedge-tailed Shearwaters breeding in the tropical western Indian Ocean. Here I examined individual fidelity to foraging sites during chick rearing and repeatability in individual flight characteristics. Prey resources are patchily distributed, however, they are not always as ‘unpredictable’ as expected (Weimerskirch 2007). Knowing that birds in this location target prey associated with seamounts (Chapter 1) and that tuna associate with these areas, I predicted high fidelity to specific foraging locations.

4.2 Materials and methods

4.2.1 Data collection

Data were collected during the course of January 2017 at Grand Anse, Réunion Island (21° 22' 30'' S; 55° 34' 07'' E) during early chick rearing. Fifteen shearwaters were equipped with CatTraQ2™ GPS loggers (Catnip Technologies, USA; 44 mm x 23 mm x 12 mm, 12 g) covered in clear heat-shrink tubing for waterproofing. The loggers were programmed to log a position every 60 min and were attached to the shearwater's tail feathers using strips of TESA® tape (Beiersdorf AG, Germany). After modification, loggers weighed less than 4.5 percent of the shearwaters body mass (logger + attachment = 14 g; average bird mass before foraging trip = 401 g).

Loggers were deployed between 18:00 – 06:00, when adult shearwaters returned to feed their chicks. After the adult had fed its chick and started exiting the burrow, it was carefully captured and equipped with a logger that was immediately turned on using a magnetic switch. Study birds were weighed using a spring balance (Pesola, Baar, Switzerland) with a precision of 5 g, before deployment and after device retrieval following chick provisioning. To easily identify equipped individuals, breast and head feathers were marked with non-toxic, white paint (Genuine Heritage Craft Products, South Africa). To record multiple trips per individual, the loggers were only retrieved after seven days of deployment. Average handling time was kept to under eight minutes.

4.2.2 Individual site fidelity

To calculate whether individuals returned to previously visited areas on successive foraging trips (following methods described in Chapter 2), the percentage overlap between the core (50% utilization distribution; UD50) and home range (95% utilization distribution; UD95) foraging areas were calculated for individual shearwaters that performed multiple short trips (described in Chapter 2), using kernelUD (*adehabitatHR;* Calenge 2006). Following Baylis et al. (2015), percentage of overlapping areas of individuals are represented as means ± standard deviation (SD).

4.2.3 Repeatability

To analyse repeated behaviour of flight characteristics within individuals, repeatability (*r*) were measured (following Nakagawa and Schielzeth 2010; Baylis et al. 2015) using the following flight characteristics: (1) maximum distance from colony (km), (2) total path length (km), (3) trip duration (d), (4) flight bearing and (6) the size (km^2) of individual core (UD50) and home range (UD95). Repeatability of these characteristics were estimated for different foraging trips of individuals (random effect) and between individuals of different sexes (fixed effect). Response variables were log-transformed to approximate a Gaussian error and the number of parametric bootstraps for interval estimation were set to 1000 (‘*rpt’* in the package *rptR;* Stoffel et al. 2017).

4.3 Results

4.3.1 Multiple trips of individuals

During early chick rearing, multiple trips were recorded for ten individuals. Six individuals performed multiple short trip cycles, lasting between three to eight trips (Fig. 4.1). Dual foraging (described in Chapter 2) was observed in the other four individuals. Individual JAN2017_47 completed eight short trips before leaving on a single long trip, JAN2017_59 made a single short trip followed by a long trip and then another two short trips thereafter, JAN2017_63 made three short trips before leaving for a long trip and JAN2017_64 made two short trips before leaving for a long trip. Where a long trip was initiated directly after a short trip, it was omitted and the overlap between the successive short trips was assessed.

4.3.2 Individual foraging site fidelity

All consecutive trips overlapped to some extent in their home range (UD95) as well as their core foraging areas (UD50). Even after long trips, shearwaters returned to areas previously visited during short trips. Only one individual's core foraging area (ID: JAN2017_59) did not overlap between the first and second trip. This occurred where the bird initially foraged to the north-west of the island, however, after a long foraging trip it changed its flight bearing and made two consecutive trips to the south-east of the island. Only one shearwater (JAN2017_66) tracked over multiple trips during chick rearing had overlapping UD95s that covered more than 50% of its home range, however, six individuals had UD95s that covered more than 30% of their active foraging area (Table 4.1). Overlap between core foraging (4.52 ± 3.94%, range 0.00 – 15.46%) and home range (38.20 ± 23.88%, range 2.67 – 91.99%; Table 4.3) areas were variable between individuals.

Tuna and billfish catches were substantially higher north west of the colony, decreasing in abundance in the pelagic waters up to the east coast of Madagascar where catch abundances increase. Catch abundance was low on the east coast of Réunion (Appendix Fig. F).

Table 4.1 Individual Wedge-tailed Shearwaters tracked over multiple foraging trips during the early chick rearing period. Mean ± SD indicated for the 50% and 95% utilization distribution percentage overlap between consecutive trips (overlap UD50 and UD95 respectively), path length (km), maximum distance from the colony (km), trip duration (d) and trip bearing.

Individual ID	n	Overlap UD50	Overlap UD95	Path length	Maximum distance	Duration	Bearing
JAN2017_42	8	3.51 ± 3.49	22.31 ± 24.07	201.8 ± 100.1	99.88 ± 103.51	1.08 ± 0.40	232.76 ± 68.55
JAN2017_59	3	3.85 ± 7.12	42.19 ± 53.47	197.41 ± 129.00	78.46 ± 58.92	0.96 ± 0.22	281.25 ± 28.53
JAN2017_60	3	7.89 ± 5.48	48.66 ± 9.20	151.33 ± 55.01	51.84 ± 26.16	1.33 ± 0.56	233.93 ± 56.38
JAN2017_63	3	5.97 ± 1.65	18.42 ± 17.23	187.67 ± 54.91	72.71 ± 20.94	0.97 ± 0.07	190.98 ± 35.40
JAN2017_64	3	3.67 ± 2.62	44.54 ± 21.38	139.13 ± 28.05	44.19 ± 12.52	0.95 ± 0.17	269.92 ± 36.00
JAN2017_66	9	6.18 ± 5.48	54.93 ± 26.97	195.9 ± 49.54	72.93 ± 21.37	0.95 ± 0.07	301.77 ± 17.11
JAN2017_68	3	5.68 ± 4.31	36.44 ± 33.76	287.66 ± 172.92	107.78 ± 48.22	0.95 ± 0.07	290.24 ± 14.05
JAN2017_69	7	3.54 ± 1.76	33.55 ± 11.12	125.34 ± 27.88	48.27 ± 12.99	1.26 ± 0.52	211 ± 27.80
JAN2017_70	6	3.36 ± 1.64	42.94 ± 14.6	143.85 ± 76.11	42.09 ± 13.58	0.78 ± 0.06	238.47 ± 33.24
JAN2017_71	2	3.07	21.23	221.43 ± 141.68	75.56 ± 49.61	0.99 ± 0.26	238 ± 7.27

4.3.3 Consistency of foraging trip characteristics

All foraging trip metrics showed low repeatability (*r* ≤ 0.32; Table 4.2), with flight bearing being the most repeatable characteristic.

Table 4.2 Repeatability (*r*), measured through intra-class correlation coefficients, among foraging trip characters (i.e. path length, maximum distance from the colony, trip duration) and the 50% and 95% utilization distribution area (UD50 area and UD95 area respectively) of Wedge-tailed Shearwaters performing multiple short trips during early chick rearing.

	r	SE	n	p
Path length	0.09	0.11	10	0.27
Maximum distance	0.10	0.12	10	0.23
Duration	0.06	0.10	10	0.36
Bearing	0.32	0.17	10	0.00
UD50 area	0.23	0.15	10	0.06
UD95 area	0.23	0.15	10	0.05

Percentage kernel utilization overlap (50% and 95% kernelUD) of home ranges between consecutive foraging trips (FT) from individual Wedge-tailed Shearwaters breeding on Réunion Island.

	Bird ID	FT1&2 overlap	FT2&3 overlap	FT3&4 overlap	FT4&5 overlap	FT5&6 overlap	FT6&7 overlap	FT7&8 overlap	FT8&9 overlap
UD 50%	JAN2017_42	1.90	10.07	5.94	0.78	2.11	3.72	0.05	
	JAN2017_59	0.00*	10.07						
	JAN2017_60	14.62	6.87						
	JAN2017_63	2.37	0.03						
	JAN2017_64	4.29*	7.99*						
	JAN2017_66	0.76	0.16	4.32	15.46	2.71	12.69	6.52	6.91
	JAN2017_68	6.68	0.58						
	JAN2017_69	2.02	3.83	3.48	2.41	6.82	2.49		
	JAN2017_70	3.14	1.40	2.75	2.77	5.86			
	JAN2017_71	2.52							
UD 95%	JAN2017_42	5.82	72.2	21.96	10.48	11.85	31.21	2.67	
	JAN2017_59	4.38*	80						
	JAN2017_60	42.15	55.16						
	JAN2017_63	30.6	6.24						
	JAN2017_64	29.42*	59.66*						
	JAN2017_66	37.76	11.38	50.07	91.99	34.58	84.26	68.97	60.4
	JAN2017_68	60.31	12.56						
	JAN2017_69	23.8	26.51	48.26	25.23	46.92	30.59		
	JAN2017_70	45.76	22.15	43.5	40.21	63.06			
	JAN2017_71	21.23							

*Indicates a long foraging trip before/after a short foraging trip

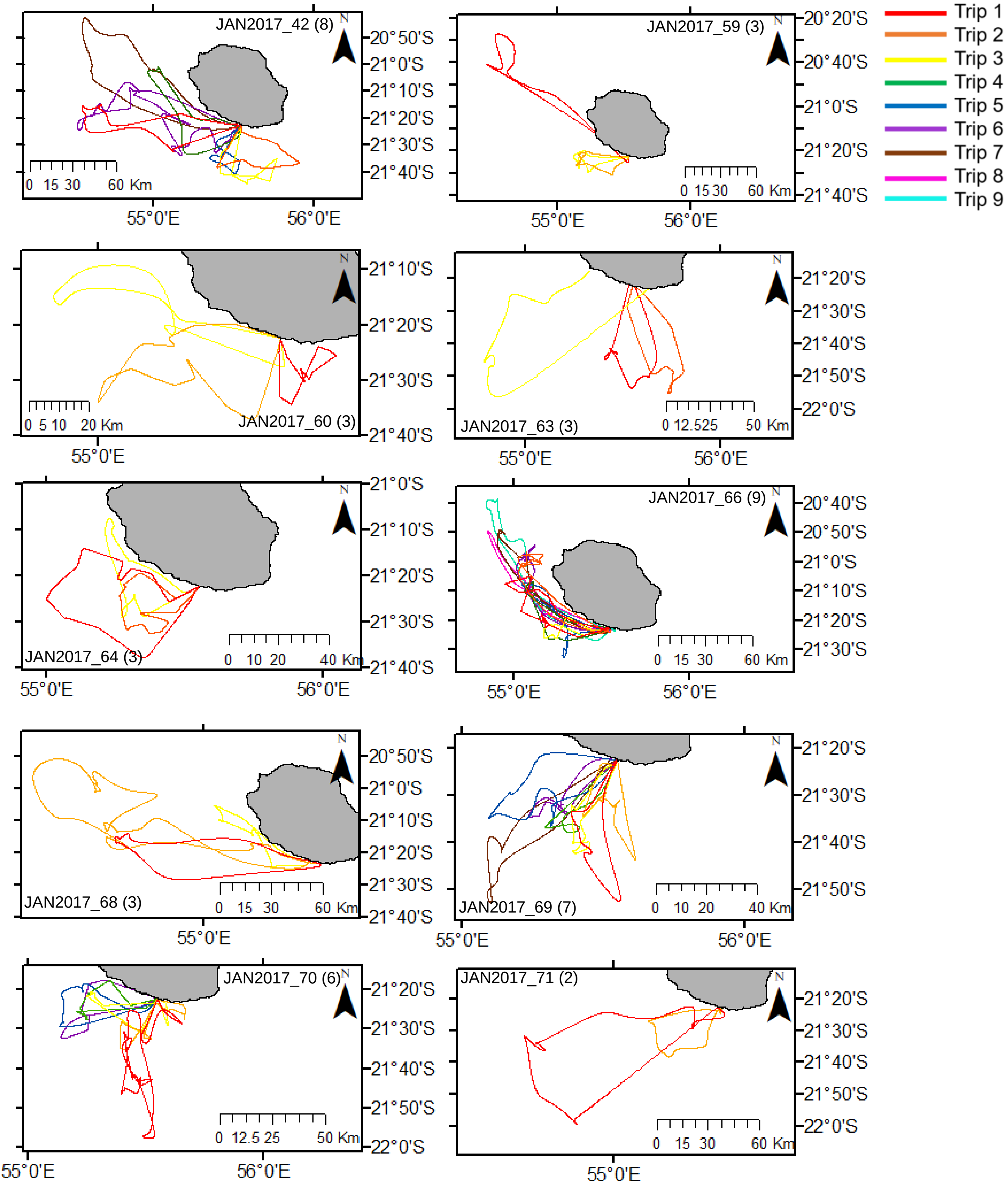


Figure 4.1 Multiple consecutive foraging trips of individual Wedge-tailed Shearwaters during the 2016/17 chick rearing period in Réunion Island. The unique identification of each individual Wedge-tailed Shearwater (and the number of trips) is indicated.

4.4 Discussion

This study demonstrates that individual Wedge-tailed Shearwaters show a high degree of variability in foraging trip characteristics within individuals during early chick rearing. However, consecutive foraging areas do overlap strongly for some individuals, indicating high site fidelity in short foraging trips near Réunion Island. During chick rearing, the individual trips of the shearwaters have a restricted home range (2158.51 ± 1936 km^2) around the breeding colony (maximum distance from the colony 69.40 ± 51.06 km). This is consistent with Jaquemet et al. (2004) who observed Wedge-tailed Shearwaters frequently foraging near Réunion Island during the breeding season. These shearwaters were regularly observed feeding in large multi-species aggregations (Jaquemet et al. 2004). It is interesting to note, that most of Réunion’s permanent FADs are anchored on the west coast of Réunion and Wedge-tailed Shearwaters have been observed in high abundances in deeper waters (500 -1000 m isobaths) near these FADs (Jaquemet et al. 2004). In this study, the shearwaters foraged south-east to north-west of the colony (bearing range: 125.46 - 317.91°; Chapter 2) and were found to make repeated trips towards the west coast in similar areas where the FADs are situated. As with other tropical seabirds (Ashmole 1971), Wedge-tailed Shearwaters also associate with sub-surface predators (Jaquemet et al. 2004). This is also true for Wedge-tailed Shearwaters foraging near Réunion, which have been observed feeding in high numbers when associating with tuna (Jaquemet et al. 2004) which in turn aggregate near FADs (Jaquemet et al. 2004; Fonteneau et al. 2013).

As indicated by multiple foraging trips made by individuals, some individuals repeatedly forage in the same areas. Shearwater JAN2017_66, for example, clearly foraged over the same relatively small area between nine consecutive foraging trips. When comparing foraging trips to oceanographic features, some individuals (JAN2017_42 (trip 7), JAN2017_59 (trip 1) and JAN2017_66 (trip 7 – 9) foraged around the Pérouse seamount. The Pérouse seamount is a shallow seamount (60 m) and has been found to concentrate zooplankton biomass along its slopes (personal communication Francis Marsac). This high concentration of zooplankton is likely to attract fish and squid (Piontkovski and Williams 1995) which are not only preyed on by tuna (of which catches have been higher than normal in this area; Appendix Fig. F) but also, the Wedge-tailed Shearwaters. Surprisingly, no shearwaters foraged to the north of the colony where catches were also high. It must be taken into confederation that traversing longline fleets may be limited in their ability to access particular fishing sites. The presence of tuna is not mutually exclusive to long line fisheries and tuna and billfish catch abundance does not necessarily reflect tuna distribution. Furthermore, longlines target deep dwelling tunas and a high longline catch does not necessarily imply that there was a high abundance of pelagic tuna near the sea surface.

Some individuals indicated low percentage overlap between consecutive foraging trips, however, for the trips after next, individuals return to areas previously visited (example individual JAN2017_42). This behaviour has often been presumed to be the result of familiarity with resources, reducing the energetic costs of foraging and consequently benefiting animals returning to known foraging areas (Piper 2011; Fagan et al. 2013; Baylis et al. 2015). The above reiterates the importance of including multiple tracks from individuals when estimating home ranges of seabird populations.

Tuna abundances respond to changes in sea surface temperatures (SST; Lehodey et al. 1997; Lu et al. 2001) and catches are negatively correlated with SST (Conand et al. 2008). Though the FADs may exhibit predictable locations of prey availability, during the shearwaters breeding season (i.e. in summer), the SST often drops suddenly (by more than 2°C) around Réunion Island which influences tuna distribution (Conand et al. 2008); which in turn may affect the repeatability of the shearwaters’ flight characteristics.

Shearwaters searching for food near the island may rely on factors such as sight, smell and memory to locate their prey on a fine scale (Nevitt et al. 1995; Weimerskirch 2007). They are thus able to recognise water masses such as those associated with seamounts (Weimerskirch 2007), which are known areas of higher productivity (Haney et al. 1996; Thompson 2008; Clark et al. 2010) or floating objects that attract potential prey (Arcos et al. 2012). This may explain why individuals repeatedly return to the same foraging areas whereas others will forage in one direction and after changing direction on the subsequent foraging trip, returning to the 'initial' foraging site. This behaviour is indicative of predictable food resources (Switzer 1993), indicating that the tropics may not always be as unpredictable as expected.

It is important to account for this variation in ecological studies by including 'enough' individuals within a population as well as to record multiple tracks of individuals over time where possible (Soanes et al. 2013). Although foraging site fidelity has now been demonstrated for a number of seabird species, very few have demonstrated consistency between years (Wakefield et al. 2015). This would be an interesting potential future research avenue for Wedge-tailed shearwaters.

CHAPTER 5

CONCLUSION AND SYNTHESIS

Seabirds live cryptic lives and many travel over several ocean basins, only coming to land to breed, and in the case of some species, to moult (Schreiber and Burger 2001). Despite the difficulties with studying seabirds in the pelagic environment, with the advancement of low-cost tracking technology and its extraordinary positional accuracy (with location errors as low as 15.4 ± 10.1 m with a fix success rate of 90 ± 26 %; Forin-Wiart et al. 2015), we can now study the fine scale foraging distributions and behaviours of seabirds at sea. Initially, the at sea foraging behaviour was limited to larger seabirds such as albatross and large petrels (Jouventin and Weimerskirch 1990; see references within Weimerskirch et al. 2007). However, the miniaturization of GPS loggers to as small as 12 g (current study) further allows us to deploy these devices on a wider range of seabirds, further increasing our knowledge of how seabirds utilize the marine environment.

In comparison to higher latitudes, very few ship based studies (Bailey 1968; Pocklington 1979; Ballance and Pitman 1999), and even fewer land based studies using tracking technology (Weimerskirch et al. 2004; Weimerskirch et al. 2005a; Catry et al. 2009b; Weimerskirch et al. 2010; Le Corre et al. 2012; Cecere et al. 2013), have been based in the tropics. Therefore, to add to the body of knowledge of marine top predators within the tropics, this study focused on the foraging ecology of Wedge-tailed Shearwaters breeding in the tropical Western Indian Ocean. More specifically, this study investigated the foraging distributions and characteristics of Wedge-tailed Shearwaters throughout different stages of their breeding periods as well as compare these metrics with different populations of Wedge-tailed Shearwaters during incubation using global positioning system (GPS) loggers. To my knowledge, this is the first study to use GPS loggers on Wedge-tailed Shearwaters (excluding a preliminary study including 10 individuals of which most trips only lasted one day; Cecere et al. 2013) to determine their fine scale at sea distribution. This study further looked at repeatability within individuals performing multiple foraging trips and assessed foraging site fidelity during chick rearing.

5.1 The foraging ecology of Wedge-tailed Shearwaters in the tropical Western Indian Ocean

Understanding the foraging distribution and flight characteristics of seabirds at sea is vitally important when interpreting the effects of environmental influences on seabird demographics (Pinaud and Weimerskirch 2002). The foraging distribution of Wedge-tailed Shearwaters indicated that they are wide-ranging foragers. Even during the breeding season when they are constrained by incubation and chick provisioning responsibilities, they cover vast distances across the open ocean. During incubation, there was no evidence of sexual segregation and shearwaters foraged predominantly south – south-west of Réunion Island, extending their range up to the south east of Madagascar (mean maximum distance: 605.00 ± 333.71 km). After incubation, there was a clear reduction in foraging range during chick rearing (mean maximum distance from colony 291.45 ± 159.88 km), which is consistent with results from other central place foragers (Fernández et al. 2001; Phillips et al. 2006; Pinet et al. 2012). In contrast to previous studies for seabirds during chick rearing (Lewis et al. 2002; Peck and Congdon 2006; Thaxter et al. 2009; Elliott et al. 2010; Pinet et al. 2012), on average females foraged closer to the colony, over a smaller area and spent less time foraging than males. Females also did not spend more time foraging during long trips than males, thus there was no indication of greater allocation of females towards self-maintenance.

Furthermore, during chick rearing, shearwaters showed a clear dichotomy between short-trip cycles (i.e. several short-trips lasting ≤ 2.54) near the island and single long-trips (>3 to 15 d) where the shearwaters foraged in distant, deeper offshore waters. These distances and durations were comparable with other tropical Wedge-tailed Shearwater populations breeding in Heron Island in the Southern Great Barrier Reef (Congdon et al. 2005; McDuie et al. 2015).

Though only a few individuals implemented this alternate foraging strategy, it is likely that other individuals within the colony in Réunion also implement dual foraging.

As discussed extensively in this thesis, during the breeding season seabirds are central place foragers and 96 % of seabird species breed in densely populated colonies (Coulson 2001). Contrary to the hypothesis that individuals from larger colonies are expected to travel further and spend more time at sea than smaller colonies (Lewis et al. 2001), when comparing the foraging distribution of Wedge-tailed Shearwaters from neighbouring islands during incubation, there was no clear indication of overall spatial segregation between shearwaters between the larger Fouquet Island colony and the smaller D’Arros Island colony. Furthermore, there were no differences in flight characteristics between shearwaters from these islands or between sexes from the different islands. However, there was low overlap between foraging hotspots. During the shearwaters breeding period, predictable phytoplankton blooms near the Seychelles archipelago occur biannually, largely influencing food availability in the surrounding areas (Monticelli et al. 2007). The higher concentration of primary production may alleviate competition to some extent in the area, supporting thousands of breeding shearwaters. At the end of the second bloom, shearwaters have been shown to disperse further out into the open ocean (Catry et al. 2009b). Surprisingly, there were no differences in flight characteristics between D’Arros and Réunion, however, the percentage overlap between active, core and ‘hot-spot’ foraging areas was substantially larger for shearwaters from Réunion. Furthermore, shearwaters from Réunion foraged over a narrower range, in comparison to shearwaters from Seychelles that had a broad foraging range and flew towards a wide range of flight bearings. This may be a result of shearwaters continuously foraging in a known area of reliable prey availability versus an area of prey found in a more patchy, unpredictable environment.

Shearwaters from both Seychelles and Réunion foraged over deep, open oceans, avoiding shallower areas. During incubation, the overall Chlorophyll *a* concentration was higher in

Seychelles, however, there was no clear indication that shearwaters selected areas of higher productivity. This could potentially be attributed to the sea surface temperature (SST) influencing foraging success (Peck et al. 2004) of Wedge-tailed Shearwaters as well as the foraging distribution by influencing the distribution of tuna (Jaquemet et al. 2004; Conand et al. 2008; Fonteneau et al. 2013).

In an ocean environment that is believed to be unpredictable, with patchy prey resources (Ashmole 1971; Au and Pitman 1986; Au and Pitman 1988; Ballance and Pitman 1999; Jaquemet et al. 2004; Weimerskirch 2007), high foraging site fidelity and repeatability within flight characteristics seems unlikely. However, though repeatability in individual flight characteristics were low, some individuals showed high site fidelity in consecutive foraging sites, repeatedly returning to the same foraging sites. I hypothesised that the shearwaters were relying on memory to locate fish aggregating devices (FAD). These FAD aggregate predatory fish species (Jaquemet et al. 2004; Fonteneau et al. 2013) which are known to drive up prey species to the surface, making prey available to surface predators such as Wedge-tailed Shearwaters.

The tracking data from this study identified important foraging areas for Wedge-tailed Shearwaters during the breeding season. It confirmed the deep coastal waters on the south-west of Réunion Island as important foraging areas for the shearwaters especially during chick rearing. The Wedge-tailed Shearwaters furthermore utilised parts of large areas of the south western Indian Ocean near the East Madagascar Current and the south east of Madagascar. Additionally, birds utilize a broad area within the Seychelles Basin which is also an important foraging area for the White-tailed tropicbird *Phaethon lepturus* (Jaquemet et al. 2004). Furthermore, the Mascarene Basin was identified as an important foraging area for shearwaters from Seychelles as well as Réunion. The deep coastal waters surrounding D'Arros and Fouquet were also important and the shearwaters' core and 'hot-spot' foraging areas are likely to become more important during chick rearing when their foraging range is likely to be restricted to areas even closer to the colonies. The Amirante Bank as well as the Amirante Basin, the pelagic waters towards north-west of Madagascar, East Somali Basin and to some extent the Mascarene Plateau were identified as important core foraging areas for shearwaters from Seychelles. These results are consistent with Le Corre et al. (2012) that identified the Seychelles Basin as well as the Mascarene archipelago as important hotspots for tropical seabirds.

Tropical seabirds mostly feed on small epipelagic prey, similar to that which is targeted by top predatory fish that form the basis of the tropical tuna fisheries (Potier et al. 2007). Clearly, the tuna fisheries and seabirds do not directly compete for the same food resources (Le Corre et al. 2003). However, though tropical seabirds may not be at risk of direct competition with fisheries or of incidental mortality on long lines like temperate or polar species (Tasker et al. 2000; Phillips et al. 2006), tropical seabirds are indirectly affected by the removal of tuna from the Indian Ocean which has been taking place at unprecedented rates since the 1980s (IOTC 2015). If tuna populations continue to decline, access of prey, through the interaction with tuna, to tropical seabirds that associate with the tuna will also decline.

Seabirds are charismatic marine top predators and are considered sentinels of the marine environment (Piatt et al. 2006; Piatt and Sydeman 2007; Ronconi et al. 2012; Amélie et al. 2016) and are indicators of change in the marine environment (Burger and Gochfeld 2004; Amélie et al. 2016). However, if we do not know how they interact with their environments we cannot make such associations. Thus, obtaining data from the at- sea distribution of seabirds in the tropics is essential when making inferences about fisheries management and conservation of pelagic ecosystems. By compiling data for the at sea distribution of seabirds we can identify important bird areas in the ocean. However, a shortage of seabird tracking data from tropical regions limits their use in informing effective marine spatial management. Nevertheless, together with studies like Le Corre et al. (2012) and current data, similar areas in the tropical western Indian Ocean have been identified to be important to seabirds and most likely other marine organisms as well.

5.2 Future research and recommendations

Globally significant populations of marine top predators have been identified in the western Indian Ocean (Ballance and Pitman 1998; Le Corre and Jaquemet 2005; Worm et al. 2005). However, these marine ecosystems have largely been influenced by human activities and anthropogenic climate change (Halpern et al. 2008). Establishing links between the foraging behaviour of marine top predators and oceanographic features will help us understand their foraging habitats and predict possible future changes in relation to these oceanographic features (Pinaud and Weimerskirch 2002). Though this study focused on the fine scale at sea movements of Wedge-tailed Shearwaters which helped identify important foraging areas for this species, for future research it will be important to include direct and indirect (stable isotopes) studies of this species' diet to further understand environmental influences on this species.

By analysing the at sea distribution of Wedge-tailed Shearwaters, this study has shown, that along with other tropical seabirds in the Indian Ocean, Wedge-tailed Shearwaters are potentially under threat by fisheries. As previously discussed, in the tropics many seabirds associate with subsurface marine top predators (Au and Pitman 1986). Within the Indian Ocean, tuna catches have increased substantially over the years (IOTC 2015). Unsustainable catches of Yellowfin tuna, over the last few years, in the high seas and in the exclusive economic zones of coastal states, has now caused this stock to be overfished (IOTC 2017). Wedge-tailed Shearwaters and other tropical seabirds are known to associate with this species (Jaquemet et al. 2004). Though the Indian Ocean Tuna Commission has set up an interim plan to rebuild the stock (Resolution 16/01), with catch limitations having started in January 2017, the effects of this measure will only be made known in 2019 (IOTC 2017). In the long term, it is important that fisheries policies and practices implement sustainable fishing, as it may have vital implications for the conservation of tropical seabirds, such as the Wedge-tailed Shearwater.

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APPENDIX

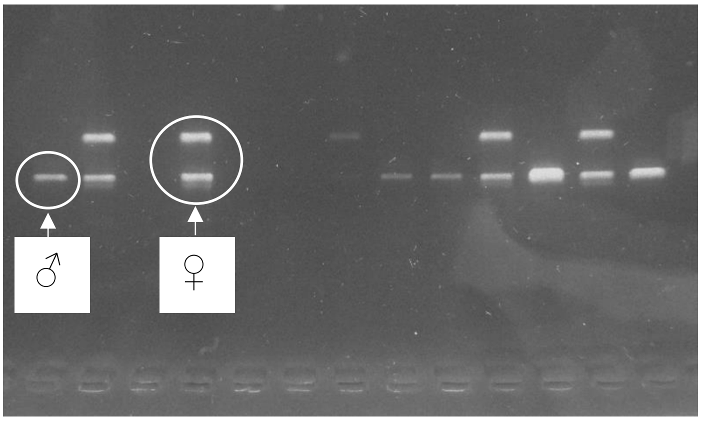

Figure A. Amplified bands were visualised under ultraviolet light to identify sexes of Wedge-tailed Shearwaters. Two bands indicate a female and one band indicate a male

Table A. 25, 50 and 90% kernel utilization distribution overlap computed with the foraging locations of Wedge-tailed Shearwaters breeding in Réunion Island, during the 2015/16 and 2016/17 breeding period over differ stages (incubation, early chick rearing and late chick rearing) for long and short trips.

		Incubation long trips	Incubation short trips	Early chick rearing long trips	Early chick rearing short trips
UD 25%	Incubation short trips	0.50			
	Early chick rearing long trips	1.20	0.29		
	Early chick rearing short trips	1.38	1.99	0.75	
	Late chick rearing short trips	0.98	0.00	0.35	0.82
UD 50%	Incubation short trips	1.25			
	Early chick rearing long trips	5.41	0.72		
	Early chick rearing short trips	4.14	9.97	2.48	
	Late chick rearing short trips	3.43	3.92	1.88	4.92
UD 90%	Incubation short trips	8.52			
	Early chick rearing long trips	30.59	4.31		
	Early chick rearing short trips	21.75	59.81	12.83	
	Late chick rearing short trips	9.81	27.42	6.81	41.00

Table B. 25, 50 and 90% kernel utilization distribution overlap computed with the foraging locations of male and female Wedge-tailed Shearwaters breeding in Réunion Island, during the 2015/16 and 2016/17 breeding period over differ stages (incubation, early chick rearing and late chick rearing) for long and short trips.

		Incubation, long trips ♀	Incubation, long trips ♂	Incubation, short trips ♀	Early chick rearing, long trips ♀	Early chick rearing, long trips ♂	Early chick rearing, short trips ♀	Early chick rearing, short trips ♂	Late chick rearing, short trips ♀
UD 25%	♂ Incubation, long trips	5.25							
	♀ Incubation, short trips	0.33	0.47						
	Early chick rearing, long trips ♀	0.65	0.99	0.65					
	Early chick rearing, long trips ♂	0	0	0	0.62				
	Early chick rearing, short trips ♀	0.76	1.16	2.46	1.06	0			
	Early chick rearing, short trips ♂	0.64	0.95	2.32	0.97	0	2.43		
	Late chick rearing, short trips ♀	0.34	1.05	0	0.52	0	0.69	0	
	Late chick rearing, short trips ♂	0.17	0.31	0	0	0	0	0	0
UD 50%	Incubation, long trips ♂	17.07							
	Incubation, short trips ♀	0.82	1.18						
	Early chick rearing, long trips ♀	1.65	3.54	1.62					
	Early chick rearing, long trips ♂	3.42	2.23	0	2.08				
	Early chick rearing, short trips ♀	2.12	3.23	6.14	2.37	0.68			
	Early chick rearing, short trips ♂	2.43	3.97	9.28	4.35	0.38	9.73		
	Late chick rearing, short trips ♀	1.82	3.16	6.24	1.91	0.75	4.84	5.11	
	Late chick rearing, short trips ♂	0.52	0.92	0	0.28	0.27	0	1.09	0
UD 90%	Incubation, long trips ♂	84.16							
	Incubation, short trips ♀	5.76	8.23						
	Early chick rearing, long trips ♀	13.17	20.17	9.05					
	Early chick rearing, long trips ♂	18.91	16.5	2.19	13.92				
	Early chick rearing, short trips ♀	10.11	16.4	31.95	9.23	6.72			
	Early chick rearing, short trips ♂	12.14	18.73	62.63	20.3	4.79	46.23		
	Late chick rearing, short trips ♀	6.47	10.02	31.21	6.96	5.19	31.08	28.08	
	Late chick rearing, short trips ♂	2.33	4.15	2.44	2.27	2.45	9.42	8.69	7.05

The female from the failed nest, travelled towards similar foraging areas (240.50 ± 25.91° from the colony) as the rest of the successful incubation trips and its “hot-spot”, core and active foraging trips overlapped with the trips for successful incubating birds (3.91, 8.61 and 68.83 % respectively; Fig C.).

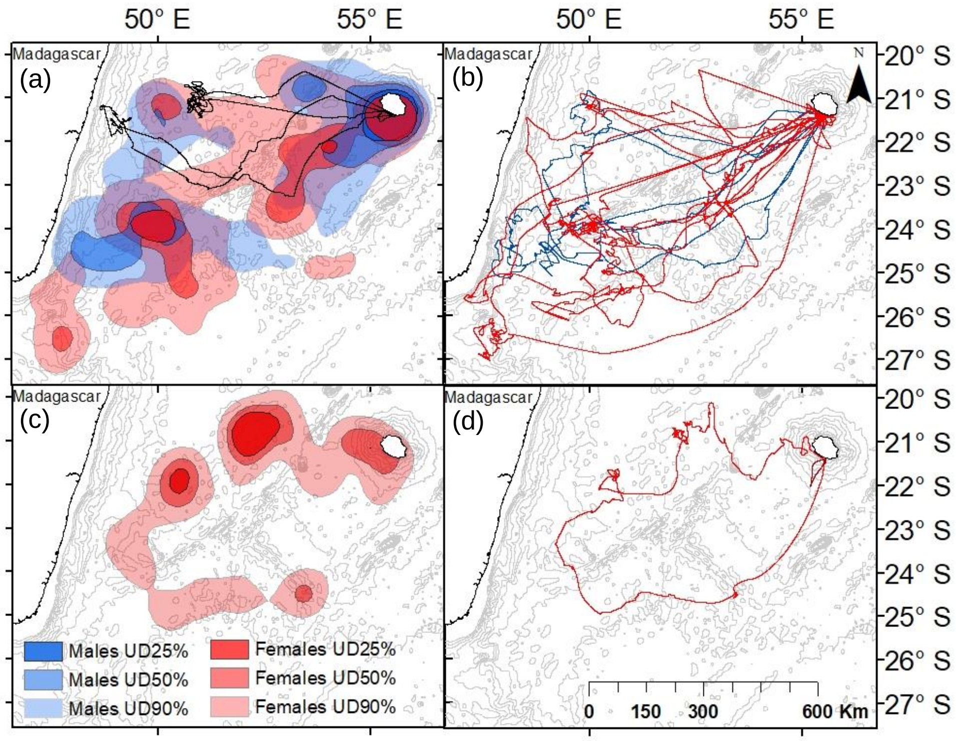

Figure B. The “hot-spot”, core and active foraging areas (25, 50, 90% utilization distribution (UD) contours) for male (blue) and female (red) Wedge-tailed Shearwaters during the 2016/17 incubation period at Grand Anse, Réunion Island for **a.** successful (GPS tracks n = 18; males n = 4; females n = 11; unknown n = 3) and **c.** unsuccessful nests (GPS tracks n = 2; females n = 2). Individual foraging tracks where sex was not determined are in black. Single tracks from individual shearwaters from successful and unsuccessful nests indicated in **b.** and **d.**

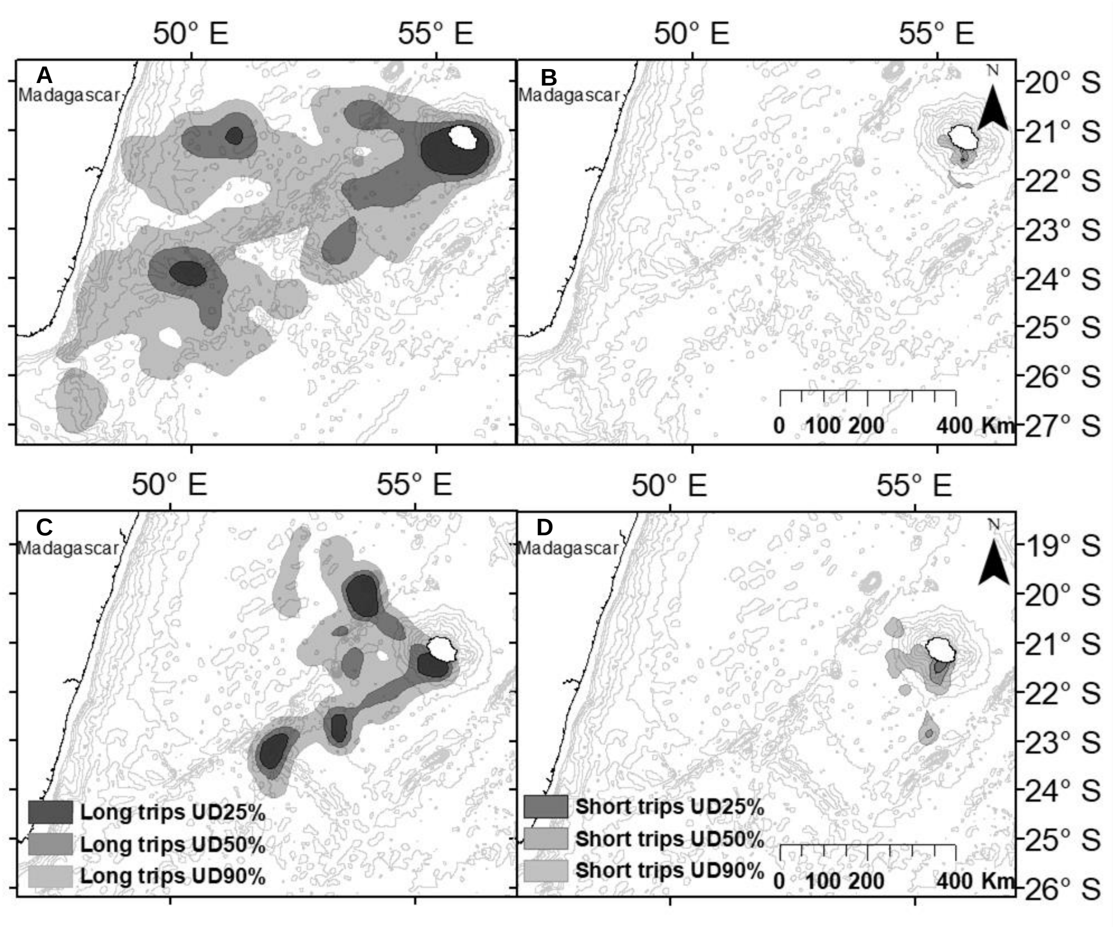

Figure C. Kernel utilization distributions (UD) of the Wedge-tailed Shearwaters on Réunion Island during the 2016/17 breeding season indicating A**.** long trips during incubation (GPS trips *n* = 14) and **B.** short trips during the late stages of incubation (GPS trips *n* = 4). Dual foraging indicated by **C.** long trips (GPS trips *n* = 5) and **D.** short trips (GPS trips *n* = 10) during early chick rearing. The “hot-spot”, core and active foraging areas during the breeding periods are represented by 25, 50 and 90% kernel density contours respectively. Isobaths (light grey lines) are at 500 m intervals between Réunion Island and Madagascar.

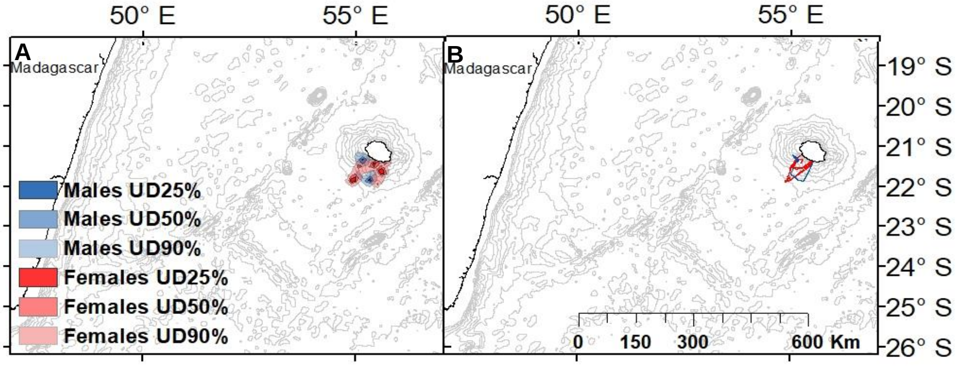

Figure D. **A.** The "hot-spot", core and active foraging areas (25, 50, 90% utilization distribution (UD) contours) for male (blue) and female (red) Wedge-tailed Shearwaters during the 2016 late chick rearing season at Grand Anse, Réunion Island. **B.** Individual tracks of Wedge-tailed Shearwaters during late chick rearing periods (GPS tracks n = 4; males n = 1; females n = 3). Isobaths (light grey lines) are at 500m intervals between Réunion Island and Madagascar.

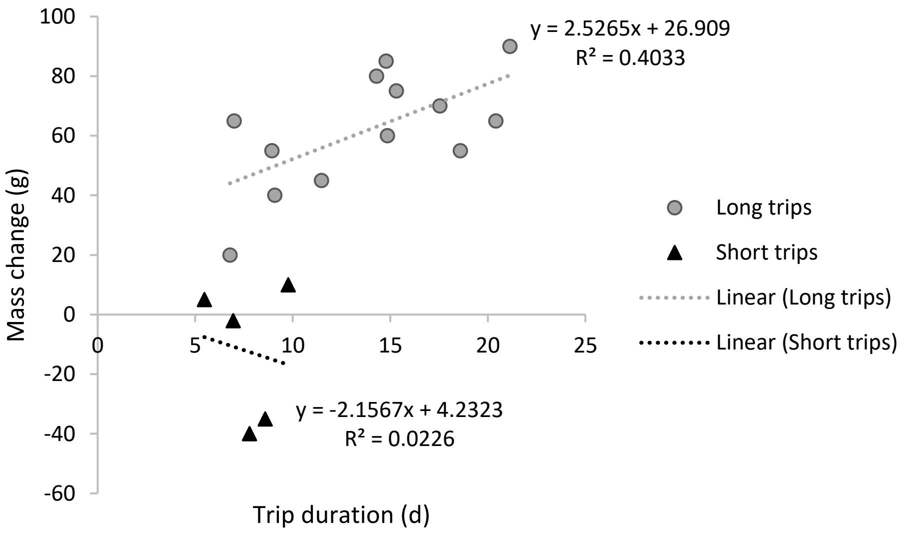

Figure E. Relationship between long trip and short trip duration and mass change after the trip of breeding Wedge-tailed Shearwaters after long and short foraging trips.

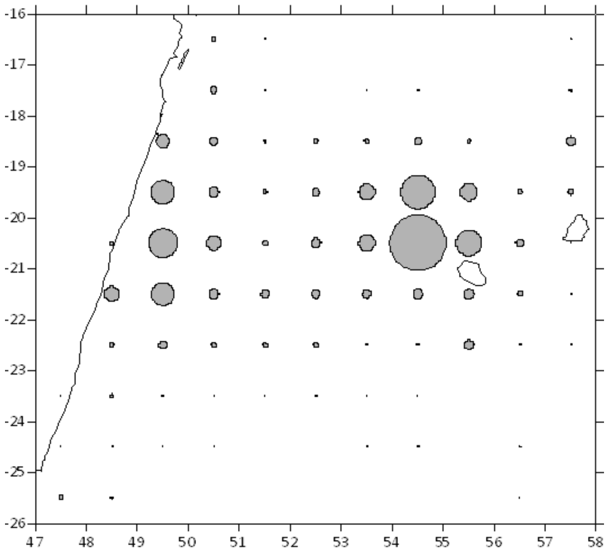

Figure F. Longline tuna and billfish catch by the Réunion fleet of 2016.