

Breeding and Foraging Ecology of Cavity Nesting Seabirds at St Helena, South Atlantic



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Summary

This thesis examines the breeding and foraging ecology of two cavity nesting seabirds in the South Atlantic: Band-rumped Storm-petrels (*Hydrobates castro*) and Red-billed Tropicbirds (*Phaethon aethereus*). Chapter 1 provides a general introduction to the thesis.

Chapter 2 characterises a range of aspects of Red-billed Tropicbird breeding ecology, against which the effectiveness of future monitoring and conservation measures can be gauged. St Helena's population represents the largest colony in the South Atlantic and an internationally important part of the global population, but has the lowest breeding success (33%) reported globally.

Chapter 3 describes the successful use of artificial nest chambers as an effective conservation tool to aid monitoring and management of cavity nesting seabird species using the Band-rumped Storm-petrel at St Helena as a case study.

Chapter 4 examines factors influencing body condition regulation in Red-billed Tropicbirds and its impact on their breeding regime at St Helena, including detailed chick growth rates from two localities in the Atlantic Ocean. Significant differences in incubation behaviour and body condition between years were identified, along with sex-specific incubation routines.

GPS tracking of the seasonally segregated population of Band-rumped Storm-petrel breeding at St Helena (Chapter 5) confirmed differentiated foraging behaviour and at-sea distribution between hot and cool season breeders, offering insights into the drivers of sympatric speciation.

Red-billed Tropicbird dietary composition and diversity at St Helena (Chapter 6) indicated highly specialised feeding that predominantly relied on juvenile epipelagic squid. Risk of bycatch was deemed low. Implications in relation to existing and potential future commercial and local fisheries practices, within its known foraging range, are discussed.

This thesis provides essential knowledge for the formulation of informed and effective conservation and management of the two seabird species in the South Atlantic, requiring urgent conservation actions.

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Chapter 3

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Chapter 1.

General Introduction

1.1. Seabirds

Seabirds comprise of approximately 350 species, representing circa 3.5% of all birds globally (Croxall *et al.*, 2012). Seabirds typically spend at least 80% of their time at sea (Hatch and Hatch, 1990) and are highly adapted to the marine environment, upon which they are dependent for at least part of their life cycle. As apex predators, seabirds forage over large geographical areas and feed at different trophic levels, and are consequently often used as indicators of the health of the marine environment around the world (Cairns, 1986; Furness and Camphuysen, 1997; Rajpar *et al.*, 2018). Through monitoring population parameters such as reproductive successes, seabirds are used as sentinels of marine ecosystem responses to environmental variability and changes (Zmudczyńska *et al.*, 2012; Zwolicki, Zmudczy and Richard, 2016), providing insights into ecosystem conditions across large regions (Hazen *et al.*, 2019).

However, seabird populations have been suffering large declines over recent decades due to threats on land and at sea (Croxall *et al.*, 2012). Understanding basic life history traits such as longevity, fecundity and survival, as well as biology and ecology of species and how these relate to the threats posed on them is essential to effectively manage and conserve species. Information on species natural history and reproductive success is critical for accurately assessing the viability of isolated populations (Leal *et al.*, 2016).

During the non-breeding period (Figure 1.1), many seabird species stay at sea and thus are less accessible to researchers during that life cycle phase. Consequently, such species often exhibit large gaps in the overall understanding by humans of many aspects of basic ecology, such as their annual cycles. During the breeding period (Figure 1.1), pelagic seabirds alternate between spending periods at sea provisioning for themselves or their offspring and periods spent on/in the nest attending an egg or chick. Accessibility can be particularly problematic for cavity and burrow-nesting seabird species that breed on steep slopes or cliffs, making regular access to breeding colonies and their cavity or burrow difficult in order to minimise unnecessary disturbance to breeding birds. Consequently, relatively little is known about the ecology of many cavity nesting species.

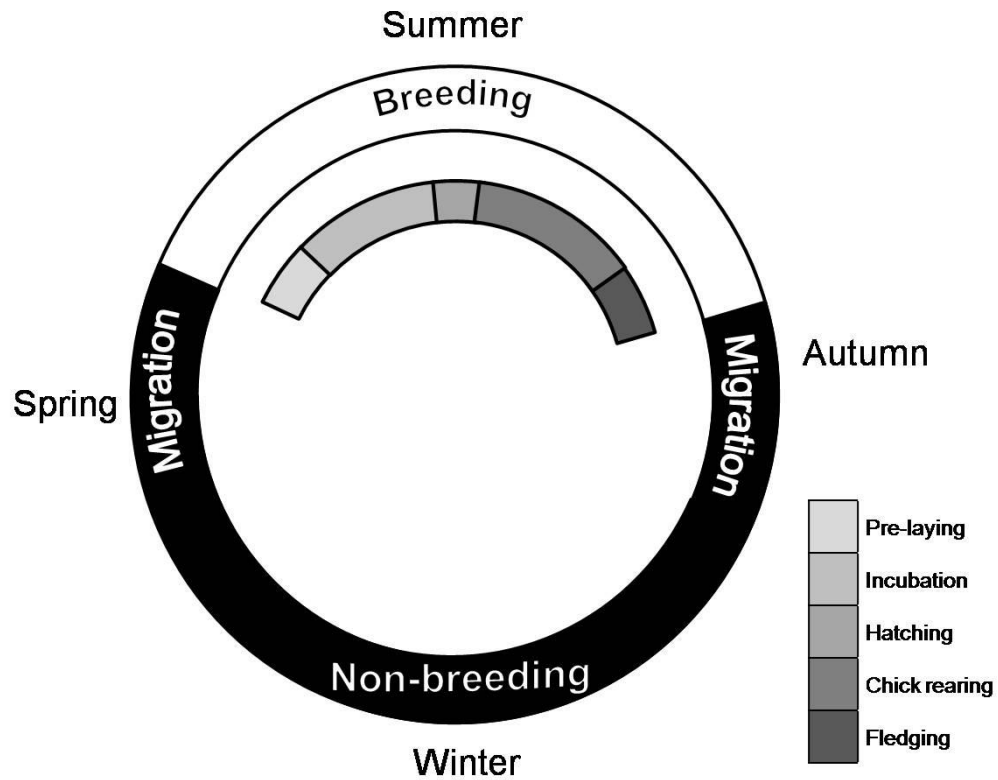


Figure 1.1. Annual cycle of a typical seabird. Timing and duration of different phases vary among species, many species do not migrate, and some species take longer than a year to complete a breeding cycle. Adapted from Hamer *et al.*, (2002).

1.1.1 Life history traits

The characteristics that affect the life cycle of a species, commonly called 'life history traits', include factors such as fecundity, longevity, sex ratio, survival, rate and timing of reproduction. Many seabird species exhibit life history traits that are unusual in other avian orders (e.g., Passeriformes). Most seabirds are socially monogamous, they often have a delayed age at first breeding, a reduced clutch size, long incubation periods, slow growth and extensive parental care (Warham, 1990; Brooke, 2004; Young and Ballance, 2023). Seabirds are also relatively long-lived, e.g., brown boobies (*Sula leucogaster*) typically live 25-30 years (Yap *et al.*, 2021), whereas most species of storm-petrel, despite their small size can exceed 30 years (Fransson *et al.*, 2023). Perhaps the most well-known example is the approximately 70 year-old female Laysan Albatross (*Phoebastria immutabilis*) called "Wisdom" (Wolfe, 2016). These extreme life history attributes make seabird more vulnerable to threats such as overexploitation, disease and environmental change. These attributes also mean seabirds are ideal to use to examine life history mechanisms, and thus enable us to better predict the impact and consequences of future environmental change on population dynamics and ecosystems.

1.1.2. Threats

Seabird populations have declined faster than any other bird taxa during the last decade (Croxall *et al.*, 2012; Paleczny *et al.*, 2015). Invasive alien species, bycatch and climate change have been identified as the top three threats thought to affect two thirds of seabird species globally (Dias *et al.*, 2019). Invasive alien species potentially affects 75% of all threatened seabird species (Croxall *et al.*, 2012). Predation of eggs, chicks and adults by invasive mammals such as rats (*Rattus* spp.) and cats (*Felis catus*) have been shown to drive many seabird population declines (Jones *et al.*, 2008; Medina *et al.*, 2011). Severe declines in seabird populations have also been driven by the increased mortality from incidental bycatch often associated with fishing. For example, bycatch in longline or trawl fisheries at South Georgia, South Atlantic were the primary cause of the 40-60% population declines in Albatross species over the last 35 years (Pardo *et al.*, 2017). Overfishing can also indirectly cause population declines through influencing food availability e.g., African penguin (*Spheniscus demersus*) and cape gannet (*Morus capensis*) (Crawford *et al.*, 2015; Grémillet *et al.*, 2016) and adversely affect breeding success through reduced prey availability (Bourgeois and Vidal, 2007). The availability of discards from fisheries can also alter seabird life history traits such as inter-annual variation in breeding performance (Louzao *et al.*, 2006).

Climate change has important ecological consequences for the marine environment. Fluctuations in food availability resulting from altering oceanographic processes can consequently affect life history traits such as timing of the breeding cycle and reproductive performance through its effect on body condition (Jenouvrier, Barbraud and Weimerskirch, 2005; Olivier *et al.*, 2005). Warmer temperatures are often associated with poorer body condition (Peck *et al.*, 2004; Connan *et al.*, 2008), lower breeding success (Inchausti *et al.*, 2003) and survival (Barbraud and Weimerskirch, 2005). The increasing in extreme weather events associated with global warming can also affect survival, reproduction and movement (Hennicke and Flachsbarth, 2009; Cadiou, Bioret and Chenesseau, 2010; Spatz *et al.*, 2017). In long-lived species such as seabirds, may exhibit a slower recovery from the impacts of climate change for example, during heat waves, the increase in heat stress an adults and chicks can cause breeding failures and temporary colony desertion, ultimately increasing a species extinction risk (Häkkinen *et al.*, 2023).

Exposure to plastic pollution is a global problem expected to affect virtually all seabird species in a few decades (Wilcox, Seville and Denise, 2015; Clark *et al.*, 2023). Other pollution sources such as from energy production and mining can directly and indirectly impact pelagic seabirds, through altering behaviour, foraging and nesting habitats (Young and VanderWerf, 2023). Renewable energy installations can directly impact seabirds via

collision and displacement (Cook *et al.*, 2018). Light pollution is a particular risk for nocturnal species such as petrels (Rodriguez, Rodriuez and Lucas, 2012), for example Leach's Storm-petrel (*Hydrobates leucorhous*) are often attracted to and get disorientated by artificial light associated with offshore oil and gas platforms, resulting in collision or stranding (Ellis *et al.*, 2013).

Conservation actions to mitigate direct and indirect impacts of threats such as invasive species may involve eradication programmes, for tackling problems such as overfishing and bycatch risk, creation of Marine Protected Areas (MPAs), no-take zones to protect populations of targeted species (Pichegru *et al.*, 2010) and/or engaging in multi-stakeholder marine spatial planning to regulate fisheries practices and reduce the impacts. However, mitigating the negative impacts of climate change on seabird species is challenging due to its large-scale global affects. As many seabird species face multiple threats and can be exposed across large areas on land and at sea due to their highly mobile nature, identifying and understanding how threats may affect seabird foraging ecology and life history traits is the first step to being able to quantify their interactions and impacts (Bertrand *et al.*, 2012).

1.2. Study Site

Isolated in the South Atlantic Ocean approximately 1900 km west from the Angola/Namibia border and 2900 km east of South America, St Helena is one of fourteen United Kingdom Overseas Territories (UKOTs) worldwide and is administered by the St Helena Government. Ascension Island is the closest land mass, located approximately 1125 km north west of St Helena (Figure 1.2).

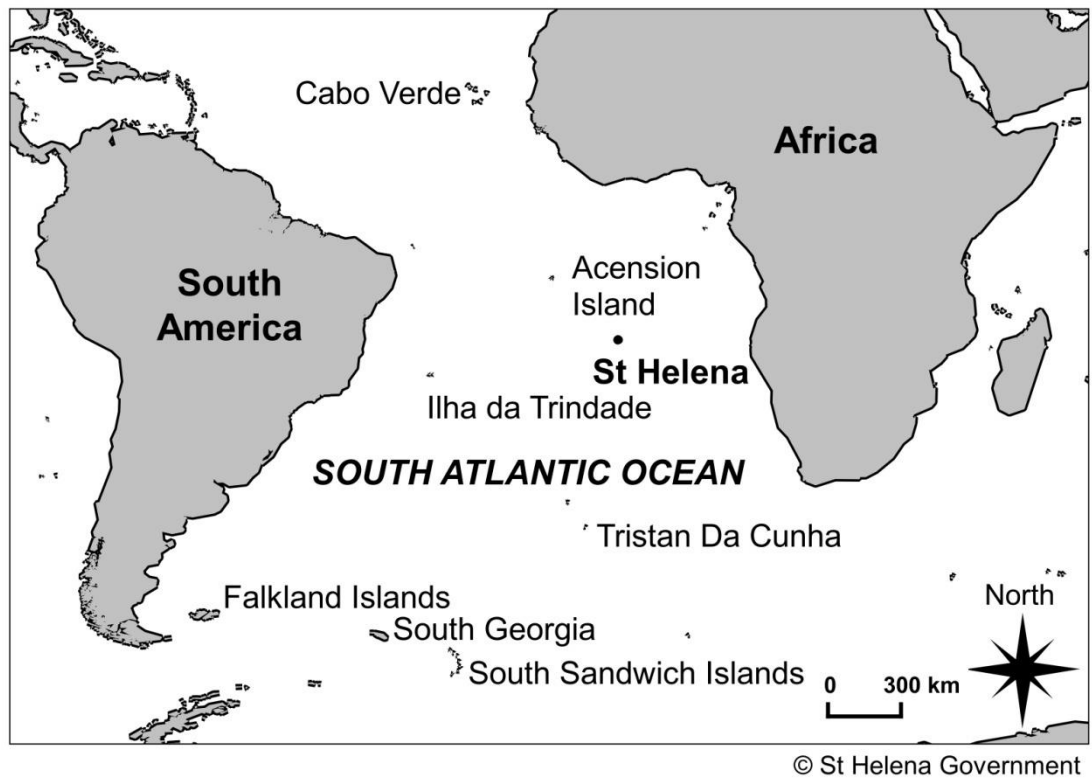


Figure 1.2. Map of the South Atlantic Ocean marking St Helena, the study site in the five data chapters of the thesis with a black dot.

This volcanic island is between 14-15 million years old (Baker, 1973), rising to 820 meters above sea-level at its highest point. Despite a relatively small land area (122 km²) it has a rich terrestrial biodiversity including, approximately 50 endemic flowering plants and ferns, 25 bryophytes, over 300 endemic invertebrate species and one endemic land bird the St Helena Plover (*Charadrius sanctaehelenae*). The island also holds at least nine native breeding species of seabird.

The Benguela current flows northward from Cape Point, South Africa, driven by the Southeast Trade winds that also drive the South Atlantic Gyre. This current system has resulted in a mix of Western and Eastern Atlantic and circumtropical marine species, with over 820 marine species recorded from St Helena (Brown *et al.*, 2019; St Helena Government, 2022). St Helena's 200 nautical mile exclusive economic zone includes two large seamounts; the closest, Bonaparte Seamount, rising 105 m below sea level and situated approximately 80 nautical miles to the west of St Helena and the shallowest; Cardno Seamount rising 77 m below sea level, situated approximately 180 nautical miles to the north.

St Helena has a narrow, shallow continental shelf which rapidly descends to abyssal depths providing key habitat for a number of large migratory mega fauna including whale

sharks (*Rhincodon typus*) (Perry *et al.*, 2020), Humpback Whales (*Megaptera novaeangliae*) which come to calf in the austral winter as well as visiting turtles and mobulid rays (Beard *et al.*, 2021). Cetaceans such as Pan-tropical Spotted, Bottlenose and Rough-toothed Dolphins (*Stenella allenuata*, *Tursiops truncates* and *Steno bredanensis* respectively) are a common sight (MacLeod and Bennett, 2007).

In 2015, the UK government committed to enhance marine protection of over 14 million km² of marine environment across the UKOTs. Known as the Blue Belt Programme, this global initiative led to the designation of the 200 nautical mile exclusive economic zone around St Helena as a MPA under the Environmental Protection Ordinance, 2016. The MPA is considered to be an International Union for Conservation of Nature (IUCN) Category VI site, aimed at "Protection with sustainable use of natural resources".

The waters around St Helena and the island itself have received relatively little research attention, with scientific advances still being made for well-known taxa such as fish (see Brown *et al.*, (2019)) and plants (see Lambdon *et al.*, (2013)). This is partly due to limited accessibility of St Helena; until recently the island could only be visited by yacht or via the Royal Mail Ship (RMS) St Helena. However, in October 2017, a small airport became operational, likely leading to an increased pressure on natural resources and the marine environment to provide food, recreation etc. Given this combination of uniqueness and changing anthropogenic threats, evidence-based advice is urgently needed to ensure resources are managed sustainably, and to enable effective management and conservation of St Helena environments and its species.

1.3. Study Species

In this thesis, I studied two highly pelagic, cavity nesting tropical seabird species, both with widespread global distributions: the Red-billed Tropicbird (*Phaethon aethereus*) and Band-rumped Storm-petrel (*Hydrobates castro*). These two species usually only come to land to breed. Both species lay a single egg during a nesting attempt and exhibit bi-parental care of the chick (Stonehouse, 1962; Bolton, 2008). The two species were identified by St Helena Government as a priority for future research due to knowledge gaps and their potential international significance following a review of seabird monitoring data gathered by St Helena Government between 2003-2011 (Beard, Clingham and Henry, 2013).

1.3.1. Red-billed Tropicbird (*Phaethon aethereus*)

Like many seabird species, Red-billed Tropicbirds are long-lived and it is assumed that 30 years is not an exceptional age (Boeken, 2016). They have a delayed maturation with an average age at first breeding around five years (Harris, 1979). Unlike other tropicbird

species (Phaethontidae) or indeed other tropical pelagic seabird species such as boobies (Sulidae) and frigatebirds (Fregatidae) that feed in flocks (Spear and Ainley, 2005a), Red-billed Tropicbirds are usually exclusive solitary feeders, which is rare among seabirds (Ballance and Pitman, 1999). Research on tropicbirds (Phaethontidae) has generally focused on the Pacific (Fleet, 1974; Spear and Ainley, 2005a, 2005b), North Atlantic (Stonehouse, 1962), and Caribbean regions (Snow, 1965; M. P. Harris, 1969; Castillo-Guerrero, Guevara-Medina and Mellink, 2011; Bright *et al.*, 2014; Soanes *et al.*, 2016). Predominantly focusing on larger accessible populations of Red-tailed Tropicbirds (*Phaethon rubricauda*) e.g., (Fleet, 1974; Vanderwerf and Young, 2014) and White-tailed Tropicbird (*Phaethon lepturus*) e.g., (Leal *et al.*, 2016; Mejías, Wiersma, *et al.*, 2017) with little attention given to Red-billed Tropicbirds.

The Red-billed Tropicbird has a pantropical distribution across the Atlantic, Pacific and Indian Oceans (Orta, 1992). The global population estimate, between 16,000-30,000 mature individuals, has a high degree of uncertainty, and the species is listed as 'Least Concern' on the IUCN Red List (BirdLife International, 2023) despite evidence of a globally declining population (Williams, 1985; Lee and Walsh-McGehee, 2000). Identified threats to the persistence of the species include predation by invasive species, habitat degradation, pollution, disease and increasing tourism (Lee and Walsh-McGehee, 2000). However, quantitative data on important basic biological and ecological traits are lacking partly due to the remote scattered nature of many colonies. In particular, there is no peer-reviewed scientific evidence on the population at St Helena.

1.3.2. Band-rumped Storm-petrel (*Hydrobates castro*)

The Band-rumped Storm-petrel species complex also known as the Madeiran Storm-petrel is a super species, previously distinguished as a single species but due to small morphological, vocal and/or genetic differences are considered as a group of close but distinct species (Allan, 1962; Taylor *et al.*, 2018, 2019). The Band-rumped storm-petrel has a global conservation status of "Least Concern", however the species also has a decreasing population trend with an estimated global population of approximately 150,000 individuals (BirdLife International, 2018). This nocturnal, cavity nesting seabird species breeds on islands across the Atlantic and Pacific Oceans, and is one of several small pelagic seabird species such as Ainley's Storm-petrel (*Hydrobates cheimnomnestes*) and Townsend's Storm-petrel (*Hydrobates socorroensis*) (Power and Ainley, 1986; Taylor *et al.*, 2018), where the evolutionary process of sympatric speciation by allochrony, a well-recognised driver of speciation, has occurred (Templeton, 1981; Friesen *et al.*, 2007; Taylor and Friesen, 2017). As an adaptation to different environmental conditions, such as food availability, populations have adjusted the timing of breeding, limiting the opportunity

for gene flow which ultimately over time lead to genetic divergence and speciation of the reproductively isolated populations (Taylor and Friesen, 2017). This Band-rumped Storm-petrel species complex breeds at distinct times of year in at least five archipelagos and/or islands in its range, St Helena included. During the “hot” season between September to December and the “cool” season from March to July (Bennett, Bolton and Hilton, 2009) storm-petrels return to St Helena to breed. Other seasonally segregated sympatric *H. castro* populations that have warranted recognition as separate species are in the Azores (Monteiro's Storm-petrel *Hydrobates monteiroi* (Bolton, 2006; Bolton *et al.*, 2008; Taylor *et al.*, 2019).

A similar re-classification has been considered for *H. castro* at St Helena, dating back to 1935 when Mathews (1935) described a separate subspecies breeding on the island (*H. c. helena*) based on morphological differences. Importantly, recent research as part of a Darwin Initiative funded project in 2016 (DPLUS018), found that despite a lack of genetic variation between the seasonal populations in the South Atlantic, both St Helena and Ascension Island populations were significantly genetically divergent from other populations examined globally (Taylor *et al.*, 2019). Indeed recent field identification guides have named the species as 'St Helena Storm-petrel' (*Thalobata [castro] helena*; Howell & Zufelt, (2019)). It is therefore highly probable that a revision of the taxonomic and conservation status of the South Atlantic populations will be made in the near future as formal recognition as a separate species is urgently needed, and thus Band-rumped Storm-petrels from St Helena and Ascension Island will hereafter be referred to as the South Atlantic Storm-petrel (*Hydrobates helena*).

1.4. Overall aims

These, both regionally and globally poorly studied seabird species, in a geographically extremely isolated location, provide a distinctive case study system to enhance our understanding of seabird biology and ecology. This thesis aimed to improve our understanding of the current conservation status of the two species at St Helena, including many basic aspects of breeding and foraging ecology that can be applied to other seabird colonies aiding conservation and management of the species globally.

1.5. Thesis structure and chapter aims

The data section of this dissertation is structured in three parts, examining breeding ecology (Chapters 2 and 3), the regulation of body condition (Chapter 4), and foraging ecology (Chapters 5 and 6).

In **Chapter 2**, I ascertain the breeding ecology, population size and examine nest site preferences of Red-billed Tropicbirds at St Helena, thus providing a comparison point for future estimates and investigations in the region.

Chapter 3 evaluates the use of artificial nest chambers by the seasonally segregated population of South Atlantic Storm-petrels at St Helena, providing quantitative evidence of their usefulness as a conservation management tool. This knowledge can inform future conservation efforts as well as offer insights into the breeding ecology of a potential newly recognised regionally endemic species.

In **Chapter 4** I examine among-year and spatial variation in body condition across the breeding cycle in the Red-billed Tropicbird. The chapter aims to provide quantitative information on the drivers of key biological life history traits to improve our understanding of the population dynamics of the species and ultimately understand the impact of environmental changes on individual fitness.

In **Chapter 5** I describe and characterise the foraging behaviour and distribution of the seasonally segregated populations of breeding South Atlantic Storm-petrels in relation to the Marine Protected Area (MPA). The aim is to better understand the drivers of allochronic speciation, and to obtain insights into potential threats and environmental factors away from the colony that may affect population parameters such as reproductive success and survival.

Finally in **Chapter 6** I ascertain the diet of Red-billed Tropicbirds from St Helena using a combination of conventional and molecular diet analysis of regurgitates. I aim to investigate and assess the risk of mortality by fisheries bycatch for the species in the region by comparing results with other dietary studies. Understanding a species dietary flexibility is increasingly important in a changing environment where prey availability may fluctuate. This chapter offers new insights into a poorly studied species and little-known region to inform future conservation.

In the general discussion (**Chapter 7**) I explore the implications of my main findings for the management and conservation of the two species in the region and identify priorities and directions for future research.

Chapter 2.

Breeding ecology, population size and nest site preferences of Red-billed Tropicbirds at St Helena, South Atlantic Ocean

This chapter has been published under the same title in *Emu - Austral Ornithology*.

2.1. Abstract

I describe the population size and breeding ecology of the Red-billed Tropicbird, *Phaethon aethereus*, a poorly studied pantropical seabird, at St Helena, South Atlantic. The population size of 81-246 pairs and 272-564 individuals identifies the study population as the largest colony of Red-billed Tropicbirds in the South Atlantic, but also an internationally important part of the global population. I estimated the survival from laying to fledging of 158 nests between 2004 and 2017 at only 33%, among the lowest values reported globally for the species. Most nest failures occur during incubation, with predation identified as the predominant cause of fledging failure. Intervals between breeding attempts were longer after successful nesting attempts than failed attempts. Previous breeding intervals and nest cavity fidelity further influenced the interval between breeding attempts, while the presence of replacement clutches did not. Multiple nest site and cavity characteristics were important predictors of cavity use, nest site selection and productivity. Management options for reducing mammalian predators to ensure the long-term viability of this important population at St Helena are discussed.

2.2. Introduction

Red-billed Tropicbirds have a pantropical distribution across the Atlantic, Pacific and Indian Oceans (Orta, 1992). Despite evidence of a decreasing population trend, the species has a global conservation status of 'least concern' with an estimated population size of 8,000-15,000 pairs (BirdLife International 2020a). Populations in the western and eastern Atlantic have been studied (Lee and Walsh-McGehee, 2000; Diop *et al.*, 2019), however there is little information on the species' abundance in the south Atlantic. The breeding range in the south Atlantic is known to extend from Fernando de Noronha and Abrolhos archipelagos in the south western Atlantic, to Ascension Island and St Helena in the central south Atlantic (Vilina *et al.*, 1994). Population estimates for this area are,

however, either data deficient (Mancini, Serafini and Bugoni, 2016), outdated (Stonehouse, 1962), or as in the case of St Helena, completely absent. Estimation of the population size and breeding productivity of the Red-billed Tropicbird population on St Helena is therefore important for its management, conservation and protection.

For seabirds, cavity nesting can provide shelter from harsh environmental conditions, supplying a more favourable microclimate for incubation and chick rearing (Mallory and Forbes, 2011). Cavities can also provide concealment and protection from predators (Rendell and Robertson, 1989; Holway, 1991). Red-billed Tropicbirds breed annually, laying a single egg in a cavity, but the influence of the physical nest site and cavity characteristics on tropicbird nest site and cavity choice has been little studied (Mejías, Wingate, *et al.*, 2017).

The primary objective of this study was to compile and update information on the St Helena Red-billed Tropicbird population, to estimate the number of breeding pairs and individuals I also examined key aspects of the species breeding ecology, breeding cycle and periodicity. Lastly, I investigated any influence of nest site and cavity characteristics on cavity occupancy, nest site selection, and reproductive performance, hypothesising that 1) less exposed and more sheltered cavities have higher nest success than those exposed to harsh environmental conditions, 2) cavities that are easy to approach and take off from (as tropicbirds are ungainly on their feet due to short tarsi), would influence occupancy, and 3) nest sites that offer a wide field of view, allowing defence against predators or competing tropicbirds would be preferred.

2.3. Methods

2.3.1. Study area and monitoring sites

I studied seven Red-billed Tropicbird colonies in St Helena in the central South Atlantic for population size estimation (Figure 2.1). Nest monitoring was conducted on Egg Island, a small offshore islet free from mammalian predators, in addition to two mainland monitoring sites: Ladder Hill and the Firing Butts.

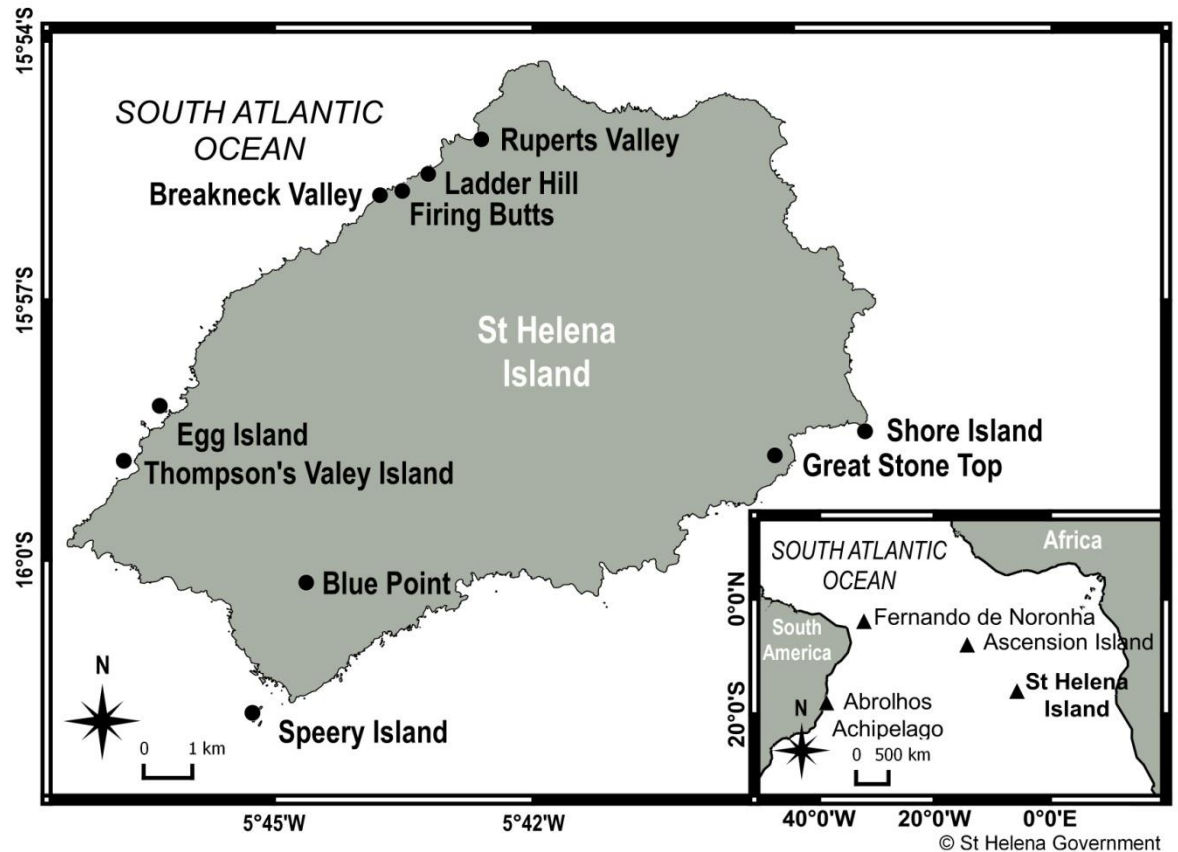


Figure 2.1. Location of Red-billed Tropicbird (*Phaethon aethereus*) monitoring sites at St Helena in the South Atlantic Ocean (insert).

2.3.2. Colony surveys

Monthly colony surveys were conducted (Table 2.1) with a minimum of two people using a telescope and/or binoculars. Each surveyor estimated incubating adults, nesting adults, nestlings, adults in territories not actively nesting and adults roosting. The average of the two counts from each surveyor was used in analyses. Scan counts were completed from a boat or set of observation points on land. Egg Island and Thompson Valley Island were visited monthly between 2005 and 2007 to conduct scan and ground counts. Ground counts were conducted on foot by slowly walking around each island searching all accessible cavities for nesting attempts. Population size was estimated as the combined number of breeding pairs, and mature individuals observed during each monthly survey, from a combination of historic and recent colony surveys as well as recent personal observations (see Table 2.1).

During colony surveys breeding activity and presence of nesting tropicbirds in cavities was often given away by fresh guano deposits, protruding tail streamers and the sound of adults and/or chicks calling. Estimation of the numbers of breeding pairs and mature individuals were derived from a combination of historic and recent colony surveys as well

as recent personal observations (See Table 2.1 for details). Adults observed in flight during colony counts were excluded. Breeding pairs were a sum of observed incubating adults (adults confirmed with an egg or chick), apparently incubating adults (adults observed sitting in a nest scrape but with no confirmed visual of an egg or chick) and nests with nestlings, assuming that each nest was attended by two adults. Adults occupying territories (adults occupying a nesting cavity but no evidence of nesting, e.g., guano covered scrape, egg or chick), adults observed roosting (birds present on the colony but not associated with a nesting cavity) and breeding pairs (assuming two adults to each nest) were pooled to provide numbers of observed individuals. Results are presented as the range of values (minima and maxima) in a month observed during the monitoring period.

Table 2.1. Historical and recent estimation of the numbers of breeding pairs and observed mature individual Red-billed Tropicbirds from colonies on St Helena. Values denote the range of total numbers counted at each monthly survey instance. *n* = number of monthly colony counts conducted.

Colony	Monitoring period	Method	<i>n</i>	Breeding pairs	Individuals
Great Stone Top	July 2013-June 2017	Scan count ^a	47 ^b	17-78	34-156
Blue Point	July 2013-June 2017	Scan count ^a	48	7-48	14-96
Shore Island	July 2013-June 2017	Scan count ^a	48	0-1	2-4
Speery Island	July 2005-June 2007	Scan count ^c	24	8-26	16-52
Egg Island	July 2005-June 2007 & July 2013-June 2017	Ground count and recent observation	24*	5-7	8-14
Thompson's Valley Island	July 2005-June 2007	Ground count	24	0-1	1-2
Ruperts Valley to Breakneck Valley	July 2005-June 2007 & July 2013-June 2017	Scan count ^c and recent observation	24*	44-85	197-240

^a observation from land, ^b one monthly survey absent due to poor weather conditions, ^c observation from boat, * excluding recent observations

2.3.3. Breeding phenology and cycle interval

I determined breeding periodicity on Egg Island by summarising monthly totals of adults incubating an egg or chick present between 2004 and 2007. Nesting activity at Ladder Hill and the Firing Butts was monitored daily from August to December 2013-2017 (see Table 2.2 for details). The breeding cycle interval was estimated as, the time period in days between the first day of incubation during one breeding period, and the next recorded

breeding attempt during a subsequent breeding period. Where the first day of incubation was not directly observed, it was estimated from hatching or fledging assuming a 43-day incubation period (Stonehouse, 1962) and an 85-day chick rearing phase (M. P. Harris, 1969).

Table 2.2. Summary of cavity and nest monitoring of mainland St Helena Red-billed Tropicbirds, 2013-2017.

Year	Number of cavities monitored	Total number of nests monitored	Minimum visual inspection	Number of cavities, cameras used	Camera deployment details
2013	24	29	daily	0	Not available
2014	28	24	daily	10	4 nests from incubation, 7 from chick rearing
2015	28	24	daily	11	5 nests from incubation, 6 from chick rearing
2016	28	16	Mondays, Wednesdays, Fridays	24	All active nesting attempts (13 cavities) plus 11 frequently used cavities.
2017	27	16	Mondays, Wednesdays, Fridays	25	Installed outside frequently used cavities for complete monitoring period

2.3.4. Nest Monitoring

Twenty-eight mainland nest cavities were marked and monitored daily via direct observation and with infra-red motion sensor cameras positioned near the entrance of cavities (see Table 2.2). Cameras capture two pictures consecutively after each trigger, with an interval of 5 seconds between triggers. Egg Island was visited a minimum of once every four weeks during the monitoring period. Adults were caught by hand and fitted with a standard alphanumeric metal ring. In addition, any breeding adults were marked on their head with a non-toxic ink dye following British Trust for Ornithology (BTO) guidelines

(licence S5526), enabling individual identification of pairs. Each nest in a cavity is given a unique nest identification number to enable estimation of the nesting cycle (incubation and chick rearing duration), nest success and productivity. Replacement clutches were identified, and the replacement interval calculated from the last date that the original failed nesting attempt was active, to the first day of incubation of the subsequent nesting attempt during the same breeding period. Feather samples were also taken from breeding adults for molecular sexing (using primers 2550F/2718R), following Fridolfsson & Ellegren (1999). Causes of breeding failure were defined into six categories, adapted from Vanderwerf & Young (2014) (Table 2.3), based on evidence from visual inspection and/or nest camera trap images.

Table 2.3. Categories of breeding failure based on the following evidence from visual inspection and/or camera trap images.

Category	Evidence
<i>broken egg</i>	occurring earlier than the expected hatch date based on the mean incubation period (43 days) and not indicative of predation
<i>abandonment</i>	intact egg incubated less than 43 days
<i>failed to hatch</i>	egg incubated longer than 43 days and failed to hatch
<i>predation</i>	remains of an egg or chick with evidence of predation, e.g., bite marks, blood, tissue, feather remains
<i>starvation</i>	where the carcass of a large chick was found
<i>neglect/exposure</i>	carcass of a small chick found with no signs of predation
<i>unknown</i>	egg or chick missing with no evidence of cause

2.3.5. Nest site and cavity characteristics

Nest site and cavity characteristics were measured using a set of 11 descriptors plus an additional two descriptors (slope and aspect) for the surrounding 5x5 metre area (Table 2.4) adapted from Einoder *et al.*, (2014). A "nest site" was defined as the location where the singular egg was laid by the female, and the "cavity" as the enclosed area around this "nest site". Cavities could contain multiple nest sites. I recorded the type of cavity (e.g., open, overhang, crevice or tube), number of entrances, and the orientation of the entrance to the nearest degree measured with a handheld GPS. Physical characteristics ($\pm 1\text{cm}$) included depth, entrance height and width, measured using a tape measurement. Volume was estimated based on $W \times H \times D$, measured from the midpoint of the nest bowl. I also recorded "slope" (whether the nest bowl was flat or had a moderate or steep slope), "substrate" (rock, gravel or soil; present or absent), and whether predators could have access to the monitoring area (mainland: true, offshore: false). To avoid disturbance, cavity characteristics were measured either before the cavity was actively used for

nesting, or after fledging when it was empty. Analysis of nest site and cavity characteristics are detailed in Table 2.5.

Table 2.4. Variables recorded for each cavity including characteristics of the surrounding site, cavity entrance and nest site.

Variable	Description
Site	
Slope	F= flat (0°); LS= low slope (1°-5°); MS = moderate slope (5°-20°), steep slope (20°-45°)
Aspect	North = 314°-45°, East = 46°-135°, South = 136°-225°, West = 226°-315°
Cavity type	Open (1), overhang (2), crevice (3) and tube (4)
Cavity entrance	
Number of entrances	1 or >1
Orientation	Mid-point of the nest entrance (degrees)
Height	Maximum height of cavity at entrance (cm)
Width	Maximum width of cavity at entrance (cm)
Nest site	
Min tunnel size	Height x width at narrowest point (cm ²)
Depth	Maximum length, outside edge of entrance to centre point of nest bowl (cm)
Chamber volume	Maximum height x depth x width from the mid-point of the nest bowl (cm ²)
Nest bowl slope	Flat = 0°, Moderate slope = 1°-5°, steep slope = 5°-10°
Substrate	Rock, (present (1) or absent (0)); Gravel, (present (1) or absent (0)); Soil, (present (1) or absent (0))
Predator access	Yes (1), No (0)

Table 2.5. Explanatory variables tested for effects on cavity occupancy, nest occurrence, hatching success and fledging success. Predicted increase (↑) and decrease (↓) of response variables for the appropriate independent variables are shown. Independent variables that were not tested towards a specific dependant variable are denoted with (X), presence (1) or absence (0).

Explanatory variable	Cavity occupancy	Nesting occurrence	Hatching success	Fledging success
Site				
Slope	↑ with slope	↑ with slope	↑ with slope	↑ with slope
Aspect	↓ with angle	↓ with angle	↓ with angle	↓ with angle
Cavity type	↓ with type	↓ with type	↓ with type (exposure)	↓ with type
Cavity entrance				
No. of entrances	↓ with >1	↓ with >1	↓ with >1	↓ with >1
Orientation	↓ with direct sun	↓ with direct sun	↓ with direct sun	↓ with direct sun
Height	↓ with height	↓ with height	↓ with height	↓ with height
Width	↓ with width	↓ with width	↓ with width	↓ with width
Nest site				
Min. tunnel size	↑ with size	↑ with size	↑ with size	↑ with size
Depth	↑ with depth	↑ with depth	↑ with depth	↑ with depth
Chamber volume	↑ with volume	↑ with volume	↑ with volume	↑ with volume
Nest bowl slope	↓ with slope	↓ with slope	↓ with slope	↓ with slope
Substrate; Rock	X	X	↓ with (1)	X
Gravel	X	X	↓ with (1)	X
Soil	X	X	↑ with (1)	X
Predator access	X	X	↑ with (1)	↑ with (1)

2.3.6. Statistical analysis

All statistical analyses were carried out in R v 4.1.2 (R Development Core Team, 2021). All Generalised linear mixed models (GLMMs, see Table 2.6 for details) were implemented in the *lme4* package (Bates *et al.*, 2015) and likelihood ratio tests (LRTs) following Lewis *et al.*, (2011) in the *lmerTest* package (Zeileis and Hothorn, 2002). Significant effects ($P < 0.05$) were plotted using the *ggplot2* (Wickham, 2016), *ggpubr* (Kassambara, 2020) and *hrbrtheme* (Rudis, 2020) R packages.

2.3.6.1. Breeding cycle interval

I used GLMMs to assess whether the interval between breeding cycles varied between sexes or consecutive breeding periods (e.g., consecutive: 2014 to 2015; non-consecutive:

2014 to 2016). Given the high level of between-season mate fidelity, nest site fidelity and their observed positive effect on breeding success in tropicbirds (Sommerfeld, Stokes and Baker, 2015), and the potential effect of breeding success on breeding cycle interval (Snow, 1965; M. P. Harris, 1969; Prys-Jones and Peet, 1980), I tested whether the interval between breeding attempts varied by 1) initial breeding outcome, 2) partner fidelity, 3) cavity fidelity, 4) initial breeding outcome and partner fidelity, 5) initial breeding outcome and cavity fidelity or, 6) initial breeding outcome, cavity fidelity and partner fidelity or, 7) partner fidelity and cavity fidelity. I excluded any individuals of unknown sex, and those that did not breed in consecutive breeding periods and/or where the breeding outcome or partner fidelity were unknown. I used a model selection approach using Akaike's information criterion adjusted for small sample size (AICc) to identify the most parsimonious model (Burnham and Anderson, 2002).

I used GLMMs to assess whether the decision to lay a replacement clutch following initial breeding failure additionally affected the breeding cycle interval, using only data from individuals that initially failed to breed. Individuals which had multiple consecutive breeding cycle intervals were also investigated further, to assess any effect of a) the previous breeding cycle interval and b) the previous breeding outcome on breeding cycle interval. I used a LRT as described above, excluding any cycles that had unknown initial breeding outcomes and/or unknown previous breeding outcomes.

2.3.6.2. Reproductive success

I excluded 54 of 212 nesting attempts where the fate of the egg or chick could not be ascertained. Estimates of hatching success (proportion of chicks hatched from eggs laid), fledging success (the proportion of chicks fledged from eggs hatched), and productivity (proportion of chicks fledged from eggs laid) were calculated assuming a 43 day incubation period and 85 day chick rearing period, respectively (Stonehouse, 1962; M. P. Harris, 1969). Daily nest survival rates were calculated using Mayfield (1975), and standard errors following Johnson (1979). Differences in breeding performance between the mainland and offshore monitoring sites were assessed by pooling historical and recent nest data. I tested for differences between years in hatching and fledging success, assessed over 5 years (2013-2017), as well as comparing mainland and offshore (Egg Island) monitoring sites using logistic exposure GLMMs (Shaffer, 2004), and LRTs to compare candidate models to a null model (Lewis, Butler and Gilbert, 2011).

2.3.6.3. Nest site and cavity characteristics

I used GLMMs to firstly examine whether occupancy of a cavity (number of individuals identified using each cavity per year) and nest occurrence (coded as 1 for presence of at

least one nest per cavity per year, or 0 for absence of any nest) on the mainland monitoring sites varied with cavity characteristics. Then I used GLMMs to investigate whether reproductive performance varied with cavity characteristics, including known replacement clutches and both mainland and Egg Island breeding attempts. Nesting attempts with either unknown outcomes and/or cavity characteristic data were excluded. For each response, I tested all possible model combinations using the 'dredge' function in R package *MuMIn* (Barton, 2020). I used a model selection approach using AICc's to identify the most parsimonious model. All candidate models were ranked based on their delta AIC value. I report models with a delta AIC ≤ 1 (Sемmens, Moore and Ward, 2009).

Table 2.6. Description of all generalised linear mixed models (GLMMs). *n* = sample size. AICc = Second-order Akaike Information Criterion. LRT = Likelihood ratio test.

Dependant and independent variables tested	Error distribution	Link function	Random effects	Fixed effect	Assessment method	<i>n</i>
Breeding cycle interval						
Breeding cycle interval = Sex	gamma	log	individual identity	-	LRT	90
Breeding cycle interval = Breeding period	gamma	log	individual identity	-	LRT	79
Breeding cycle interval = initial breeding outcome	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = partner fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = cavity fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome and partner fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome and cavity fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome + cavity fidelity and partner fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = partner fidelity and cavity fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome+ partner fidelity + cavity fidelity + initial breeding outcome and partner fidelity + initial breeding outcome and cavity fidelity + initial breeding outcome + cavity fidelity and partner fidelity + partner fidelity and cavity fidelity	gamma	log	individual identity	-	AICc	70

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Breeding cycle interval = Previous breeding cycle interval	gamma	log	individual identity	Breeding outcome	LRT	33
Breeding cycle interval = Previous breeding outcome	gamma	log	individual identity	Breeding outcome	LRT	30
Breeding cycle interval = Replacement clutch	gamma	log	individual identity	-	LRT	66
Productivity						
Hatching success = Location	binomial	Logistic exposure	Cavity identity	-	LRT	135
Hatching success = Year	binomial	Logistic exposure	Cavity identity	-	LRT	107
Fledging success = Location	binomial	Logistic exposure	Cavity identity	-	LRT	99
Fledging success = Year	binomial	Logistic exposure	Cavity identity	-	LRT	84
Nest site and cavity characteristics						
Adult occupancy = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope	Poisson	Square root	cavity identification and year	-	AICc via dredge	136
Nest occurrence = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope	binomial	probit	cavity identification and year	-	AICc via dredge	136

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Hatching success = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope + Substrate + Predator access	binomial	cloglog	cavity identification and year	-	AICc via dredge	125
Fledging success = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope + Predator access	binomial	cloglog	cavity identification and year	-	AICc via dredge	81

2.4. Results

2.4.1. Population size and breeding phenology

A total of 81-246 breeding pairs and 272-564 mature individuals were observed in St Helena per each (monthly) survey during the study period (Table 2.1).

Fifty-one nests with eggs and 18 chicks were monitored on Egg Island (Figure 2.2). Red-billed Tropicbirds were observed breeding every month of the year, with a peak in egg laying from July to January. The highest average number of eggs laid occurred in September, and the lowest in March and April. The number of chicks observed peaked from October to April, with the highest average number of chicks occurring in February and the lowest since May to September.

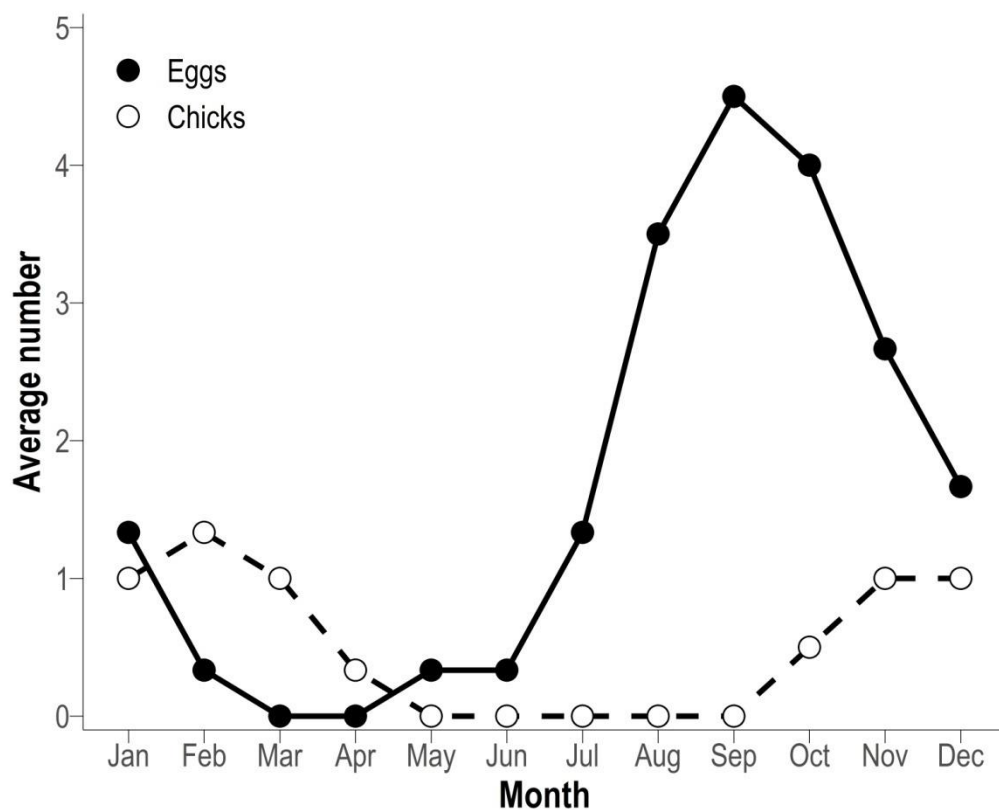


Figure 2.2. Breeding phenology of Red-billed Tropicbirds on Egg Island, St Helena from October 2004 to August 2007.

2.4.2. Breeding cycles and intervals

Mean incubation period was 42.9 days (range 37-46 days, $n = 31$), and mean chick

rearing period was 92.6 days (range 89-103 days, $n = 13$), giving a mean breeding cycle of 135.5 days (range 126-149 days). The overall average breeding cycle interval identified between 2013 and 2017 from 50 individuals, over five breeding periods was 416 ± 177 days (range 222-1433 days, $n = 91$, Figure 2.3), 87% of which were bred in consecutive breeding periods with a mean interval of 357 ± 50 days (range 222-465 days, $n = 79$).

There were significant differences in breeding cycle interval between consecutive breeding periods (LRT; $\chi^2_3 = 11.807$, $P = 0.008$, $n = 79$), but not between the sexes (LRT; $\chi^2_1 = 0.077$, $P = 0.782$, $n = 90$). The length of the breeding cycle interval between 2016 and 2017 was on average 44 days shorter than between 2013 and 2014 (2016-2017: mean 324 days, range 277-352 days, $n = 12$; 2013-2014: mean 368 days, range 222-465 days, $n = 24$) reflecting initial breeding outcomes (in the later period (2016-2017), all initial breeding attempts failed, whereas in the earlier period (2013-2014) some chicks fledged, see Table 2.7).

After accounting for repeated measures of an individual's breeding cycle interval, initial breeding outcome and nest site cavity fidelity explained the largest variation in breeding cycle interval length (Table 2.8). Breeding cycle interval was significantly longer when the initial breeding attempt was successful ($\beta = 0.075 \pm 0.035$ SE, $R^{2m} = 0.111$, $R^{2c} = 0.404$, $t = 2.125$, $P = 0.034$, $n = 70$). Adults that initially successfully fledged a chick took an average of 41 days longer to nest in the following breeding period (mean 391 ± 57 days, range 313-465 days, $n = 18$) compared with adults that initially failed to breed (mean 350 ± 40 days, range 222-415 days, $n = 52$, Figure 2.4). There was no significant difference in the breeding cycle interval between individuals, which initially failed to breed and laid a replacement clutch and those which did not lay a replacement clutch after initial breeding failure (LRT $\chi^2_1 = 1.371$, $P = 0.242$, $n = 66$).

After accounting for the outcome of the initial breeding attempt and repeated measures of individuals, an individual's breeding cycle interval was not significantly influenced by the outcome of the previous breeding cycle's breeding attempt (LRT; $\chi^2_1 = 3.548$, $P = 0.060$, $n = 30$) but was negatively influenced by the length of the previous breeding cycle interval; the longer the previous breeding cycle interval, the shorter the breeding cycle interval in the following breeding period ($\beta = -0.142 \pm 0.014$; LRT; $\chi^2_1 = 38.706$, $P < 0.001$, $n = 33$).

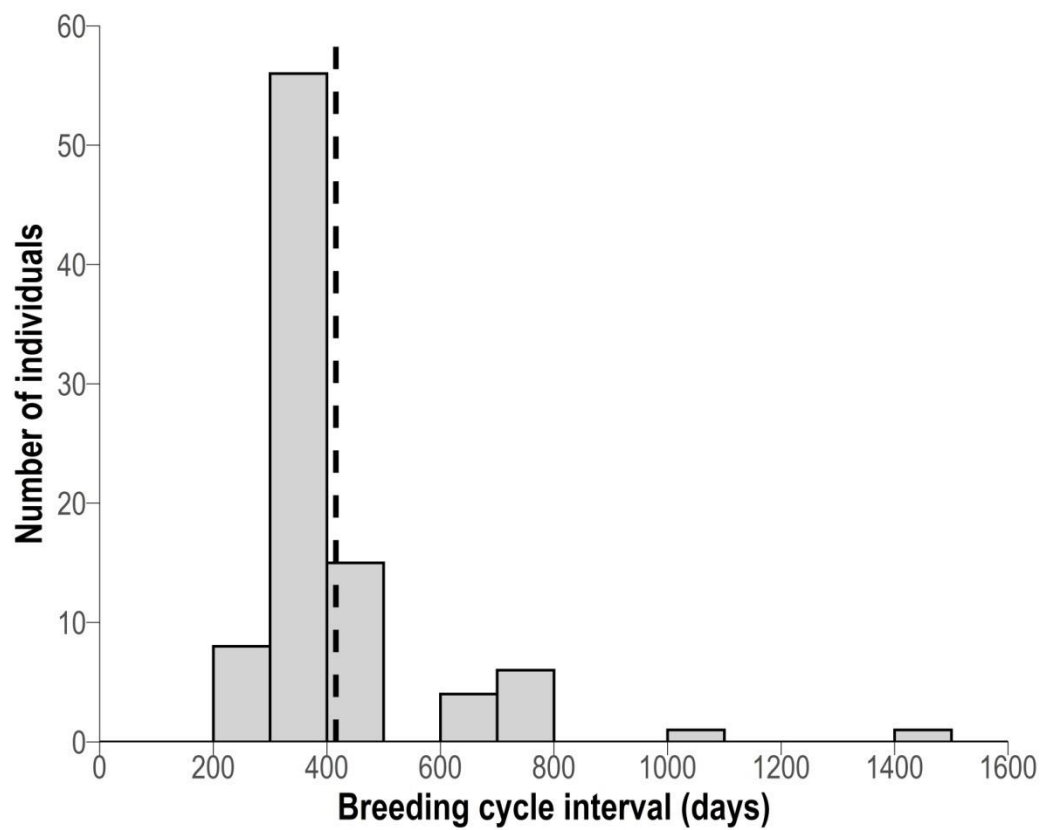


Figure 2.3. Frequency distribution of breeding cycle intervals of individual Red-billed Tropicbirds 2013-2017 ($n = 91$), based on recapture of individuals whilst breeding and estimation of laying dates. Dashed black line represents the mean (416 ± 176 days SD).

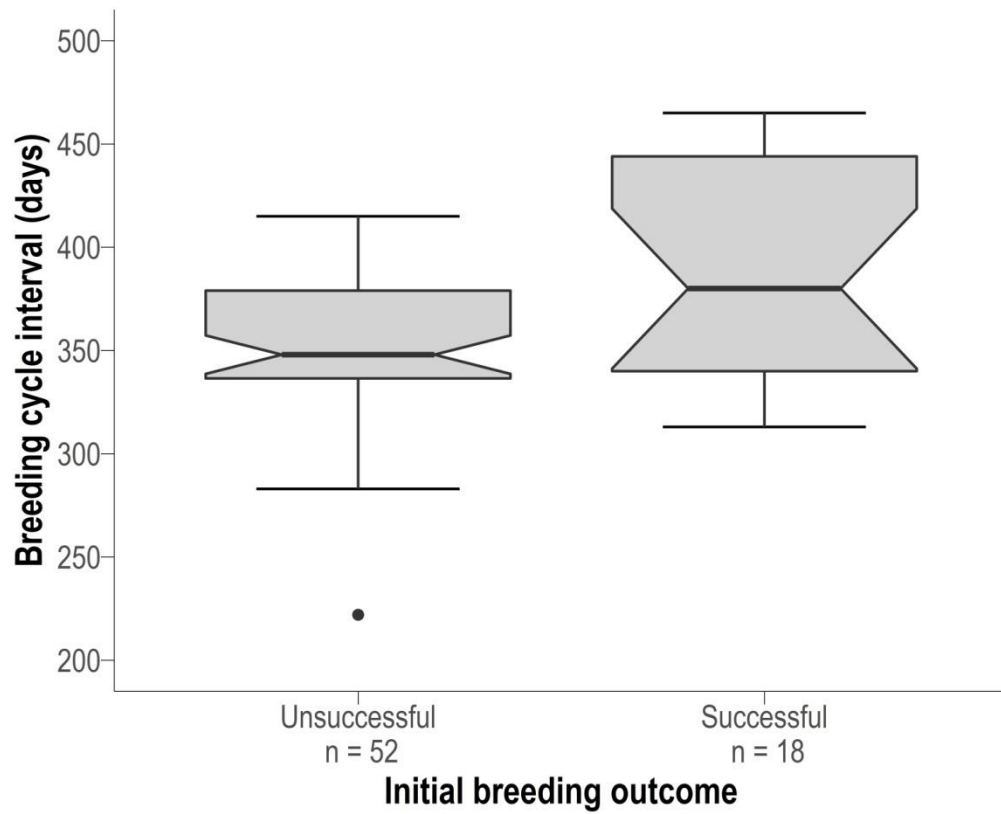


Figure 2.4. Breeding cycle interval (duration of time between nesting attempts in different breeding periods) for successful and unsuccessful nesting attempts of Red-billed Tropicbirds in St Helena between 2013-2017. Unsuccessful = the interval between the date when the prior nest failed and the first egg date of the subsequent breeding attempt. Successful = the interval between the date when the prior nest successfully fledged a chick and the first egg date of the subsequent breeding attempt.

Table 2.7. Summary of Red-billed Tropicbirds nests monitored on St Helena, 2013-2017. Mayfield daily nest and chick survival estimates (± 1 standard error). Hatching success is the proportion of chicks hatched from eggs laid, fledging success is the proportion of chicks fledged from eggs hatched and productivity is the proportion of chicks fledged from eggs laid.

	Monitoring period					Sum
	2013	2014	2015	2016	2017	
Total eggs laid	27	30	24	22	25	128
Daily nest survival	0.989 $\pm$ 0.004	0.984 $\pm$ 0.005	0.987 $\pm$ 0.005	0.978 $\pm$ 0.006	0.990 $\pm$ 0.004	
Total chicks hatched	20	19	16	10	19	84
Hatching success (%)	74	63	67	45	76	
Daily chick survival	0.978 $\pm$ 0.006	0.986 $\pm$ 0.005	0.979 $\pm$ 0.006	0.974 $\pm$ 0.009	0.998 $\pm$ 0.001	
Total chicks fledged	5	9	5	2	17	38
Fledging success (%)	25	47	31	20	89	
Productivity (%)	19	30	21	9	68	

Table 2.8. Model selection table evaluating the effect of initial breeding outcome, cavity fidelity and partner fidelity on the breeding cycle interval of Red-billed Tropicbirds 2013-2017 ($n = 70$). k : number of estimable parameters; AICc: Akaike's information criterion; Delta AICc: difference in AICc units to the most parsimonious model; wAICc: relative weight of evidence for each model.

Model	k	AICc	Delta AIC	wAICc
Initial breeding outcome + Cavity fidelity	5	733.713	0.000	0.303
Initial breeding outcome	4	733.967	0.254	0.266
Initial breeding outcome + Partner fidelity	5	735.584	1.871	0.119
Initial breeding outcome + Partner fidelity + Cavity fidelity	6	735.795	2.082	0.107
Cavity fidelity	4	735.799	2.086	0.107
Cavity fidelity + Partner fidelity	5	737.063	3.350	0.057
Partner fidelity	4	738.874	5.161	0.023
Null	3	739.235	5.522	0.019

2.4.3. Productivity

Altogether 158 nests were monitored 2004-2017, showing a hatching success of 63%, fledging success of 52%, and overall productivity of 33%. Hatching success on the mainland (64%) was marginally higher than offshore (61%) on Egg Island, LRT; $\chi_1^2 = 0.305$, $P = 0.581$, $n = 135$), with no significant difference between years (2013-2017; LRT; $\chi_1^2 = 0.002$, $P = 0.961$, $n = 107$). Fledging success was substantially higher offshore on Egg Island (77%) than on mainland St Helena (41%, LRT; $\chi_1^2 = 4.910$, $P = 0.027$, $n = 99$), and ranged from 20% in 2016 to as high as 89% in 2017 (LRT; $\chi_1^2 = 26.638$, $P < 0.001$, $n = 84$), driven by large between-year variations in daily chick survival (Table 2.7).

2.4.4. Causes of failure

I identified the cause of 88% of breeding failures during the study (Table 2.9), with 53% of failures occurring during incubation; predominantly abandonment (42%), and 47% during chick rearing; mostly predation (58%). Of 26 known nest predation events, 42% (11) were caused by feral or domestic cats (*Felis silvestris catus*), 8% (2) were caused by domestic dogs (*Canis familiaris*), 4% (1) were caused by rats, however predators remained unidentified for 12 events. Out of nine identified instances where fights with interlopers caused indirect disturbances leading to nest failure, seven involved other Red-billed Tropicbirds competing for nesting cavities (resulting in five broken eggs, one abandoned egg, and one neglected chick). Two free roaming domestic dogs caused significant disturbance to two breeding pairs, leading them to abandon their incubation.

Table 2.9. Causes of Red-billed Tropicbird nest failures on St Helena (mainland only) 2013-2017.

Cause	Number		Percentage
	Incubation	Chick Rearing	
Predation	0	26	27%
Abandoned	21	1	23%
Broken egg	19	-	20%
Unknown	7	4	12%
Neglect/exposure	0	8	8%
Starvation	-	6	6%
Failed to hatch	3	-	3%
Total	50	45	100

2.4.5. Incidence of replacement clutches

I identified 13 replacement clutches 2013-2017, laid after initial breeding failure, with an average interval of 42 ± 9 days (range: 27-53 days). Six replacement clutches (46%) were laid after loss of an egg, whereas seven replacement clutches (54%) were laid after loss of a chick. Ten pairs were identified as the same combination of individuals as in the first nesting attempt (i.e., confirmed mate fidelity), while the identity of one or both partners in three additional re-nesting attempts remained unverified. Ten pairs (77%) used the same nesting cavity to lay a replacement clutch, whereas three pairs (23%) chose a different cavity despite their previous nesting cavities being vacant at the time of laying the replacement clutch. Two of the three pairs were individuals breeding with the same partner, and the third could not be verified.

2.4.6. Nest site and cavity characteristics

My full dataset comprises 125 breeding attempts in 46 nest sites from 41 cavities 2013-2017. A maximum of eight individuals were identified using a given cavity within a year. Most nest sites were located on flat or low slopes, and none were recorded on steep slopes. After accounting for repeated observations each year and of each cavity, the model that best explains whether a chamber is occupied or not by Red-billed Tropicbirds in a given year (Table 2.10), included the type of cavity, the number of entrances to the cavity, the size of the tunnel to the nest site, the volume of the nest chamber, the slope of the nest bowl and the aspect of the site. The best model suggested that more enclosed cavities (such as tubes), exhibiting fewer entrances, smaller tunnels, larger chamber volumes, and nest bowls with a flat slope were more likely to be used ($R^{2m} = 0.269$, $R^{2c} = 0.407$, $n = 136$, Table 2.10a). Likewise, the model that best explains nest occurrence in any given year includes the cavity type, the number of entrances to the cavity, the width of

the cavity entrance as well as some influence of tunnel size. Specifically, nest occurrence on mainland St Helena was positively related to enclosed cavities with a single wide entrance ($R^{2c} = 0.133$, $R^{2m} = 0.300$, $n = 136$, Table 2.10b).

Soil at the nest site and the slope of the site around the cavity were important characteristics determining hatching success. The presence of soil (Figure 2.5) and flatter slope around the site, although slope was not significant, it increased the likelihood that an egg would hatch ($R^{2m} = 0.050$, $R^{2c} = 0.052$, $n = 125$, Table 2.10c). The nest bowl slope was a key component in predicting fledging success, suggesting higher fledging probability in flat nest bowls, along with potential, albeit non-significant influence of cavity orientation and tunnel size ($R^{2m} = 0.223$, $R^{2c} = 0.364$, $n = 81$, Table 2.10d, Figure 2.5).

Table 2.10. Significance and variable importance of generalised linear mixed model (GLMM) selection of specific nest site and cavity characteristics with cavity occupancy, nest site selection and reproductive performance of Red-billed Tropicbirds at St Helena 2013-2017. Cavity identification and year were included as random effects in all models to control for repeated measures.

a) Cavity occupancy^a				
Predictors	estimate	std error	z	P value
Cavity type	0.266	0.091	2.908	0.004
Aspect	0.176	0.103	1.704	0.088
Number of entrances	-0.418	0.130	-3.227	0.001
Tunnel size	-1.195	0.079	-2.472	0.013
Volume	0.240	0.071	1.080	0.001
Nest bowl slope	0.457	0.152	3.007	0.003
b) Nest occurrence^b				
Cavity type	0.403	0.178	2.256	0.024
Number of entrances	-0.559	0.191	-2.928	0.003
Width	0.766	0.351	2.185	0.029
Tunnel size	-0.626	0.340	-1.839	0.066
c) Hatching Success^c				
Slope	-0.314	0.039	-1.538	0.124
Soil	0.614	0.286	2.146	0.032
d) Fledging success^d				
Nest bowl slope	-2.029	0.843	-2.407	0.016
Orientation	-0.377	0.208	-1.808	0.071
Tunnel size	0.683	0.403	1.694	0.090

^a Poisson error distribution and sqrt link function, $n = 136$

^b Binomial error distribution and probit link function, $n = 136$

^c Binomial error distribution and cloglog link function, $n = 125$

^d Binomial error distribution and cloglog link function, $n = 81$

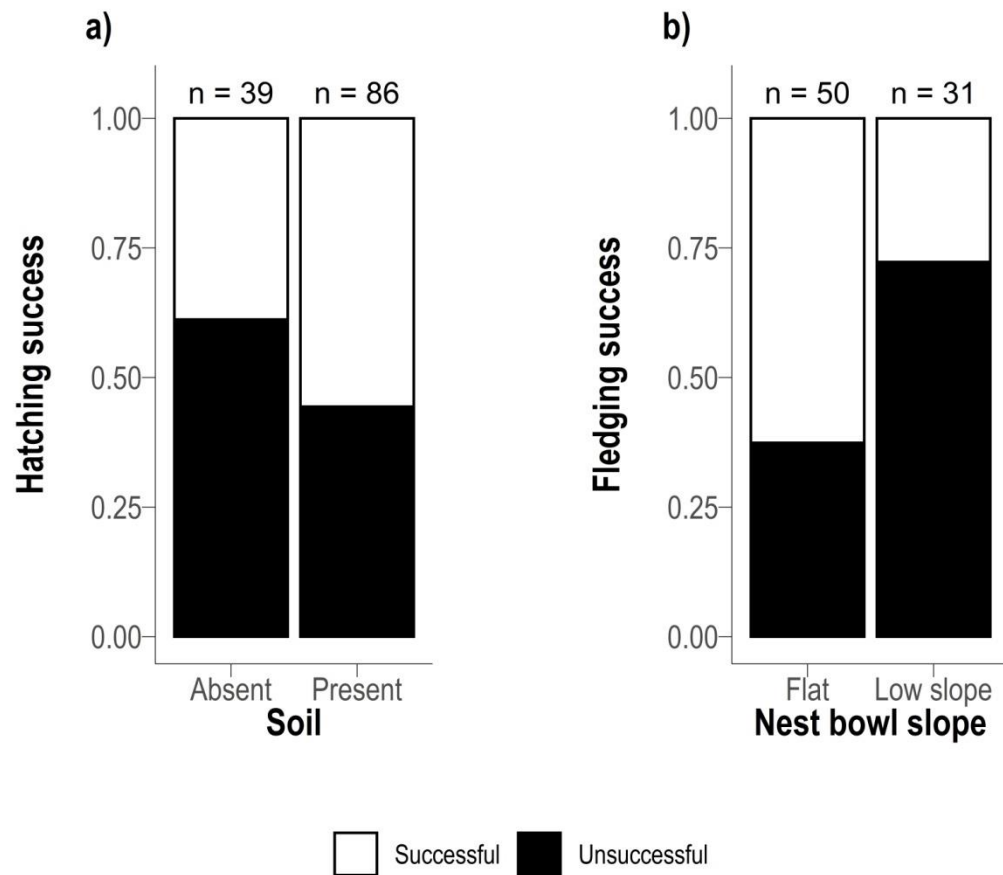


Figure 2.5. Stacked bar charts showing the proportion of successful and unsuccessful nests in a) soil substrate and b) each nest bowl slope. Successful breeding attempts shown in white, and unsuccessful breeding attempts in black.

2.5. Discussion

My findings show that the population of Red-billed Tropicbirds on St Helena is regionally and globally important for the persistence and conservation of the species. However, the low observed breeding productivity, and threats identified here in this population are cause for concern, and shared with *Phaethon sp.* populations elsewhere (Castillo-Guerrero, Guevara-Medina and Mellink, 2011; Sommerfeld, Stokes and Baker, 2015; Madden, 2019).

2.5.1. Population estimates

This study is the first to quantify the number of breeding pairs and mature individuals of Red-billed Tropicbirds on St Helena. The minimum of 32-246 pairs and 106-564 mature individuals observed in the monthly surveys is likely to be an underestimate, however it suggests that the St Helena population probably is the largest colony in the South Atlantic,

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compared to estimated 10 individuals on Fernando de Noronha, 538 individuals in the Abrolhos Archipelago (Mancini, Serafini and Bugoni, 2016) and 50-100 pairs on Ascension Island (Stonehouse, 1962). St Helena harbours at least 1% of the global population of Red-billed Tropicbirds, and at least 35% of the South Atlantic population. These population estimates exceed the Important Bird Area (IBA) threshold (BirdLife International 2020b), making St Helena's population a "regionally important congregation" of Red-billed Tropicbirds in the South Atlantic (criterion B3a), and an internationally important part of the global population ($\geq 1\%$; criterion A4).

2.5.2. Breeding phenology and cycle interval

From colony surveys, Red-billed Tropicbirds were found breeding throughout the year on St Helena, with a peak in egg laying in September similar to that described from the Galápagos (Snow, 1965) and nearby Ascension Island (Stonehouse, 1962). This phenology differs from populations in Senegal (Diop *et al.*, 2019), the Cape Verde archipelago and Mexican breeding colonies (e.g., Clarion Island (González-Zamora *et al.*, 2017), San Jorge Island (Mellink and Palacios, 1993) and Farallon de San Ignacio (Castillo-Guerrero, Guevara-Medina and Mellink, 2011)), which have differing seasonal productivity patterns ranging from October to June. Variations in annual cycles across populations are likely due to oceanographic conditions and food availability (Weimerskirch, 2007; Diop *et al.*, 2019).

Individual Red-billed Tropicbirds on St Helena typically have a consistent annual breeding cycle, supporting previous suggestions by Stonehouse (1962), Snow (1965) and Harris (1969). However, some individuals were recorded as absent in one cycle period, but appearing in subsequent cycle periods, suggesting that individuals may skip a breeding cycle under certain conditions (Ashmole, 1965; Chastel, 1995; Jouventin and Dobson, 2002; Dawson, 2008). The breeding periodicity of successful breeders was ca. ~ one month longer than that of failed breeders, reinforcing the theory that a major driver of breeding phenology in Red-billed Tropicbirds is linked to breeding outcomes (see Stonehouse 1962; Snow 1965; Harris 1969; Prys-Jones and Peet 1980). In addition, I provide evidence that an individual's breeding phenology in a given year is also influenced by time since the last breeding attempt (previous breeding interval) and by nest site fidelity. My findings suggest that the shorter breeding periodicity observed in repeated unsuccessful breeders may not be sustainable over multiple breeding cycles, hence the negative influence of previous breeding intervals on periodicity.

2.5.3. Reproductive success

Hatching success was similar across the monitoring sites and over the years. In contrast, estimates of fledging success showed considerable spatial and temporal variations, with

lower success at sites, with mammalian predators being present. On Egg Island, a site with no mammalian predation, breeding success was 47%, whereas at the mammal-impacted sites on mainland St Helena breeding success was only 26%. I observed substantially higher fledging success in 2017, possibly due to climatic and/or food availability fluctuations (Schreiber, 1994; Blight *et al.*, 2010). As a consequence, resulting variation in breeding success among years was primarily driven by chick survival, consistent with previous studies and between different sites within the same locality (Snow, 1965; M. P. Harris, 1969; Hernández-Vázquez *et al.*, 2018; Diop *et al.*, 2019),

St Helena's hatching success of 63% is low compared with 75% in the Gulf of California, Mexico (Castillo-Guerrero, Guevara-Medina and Mellink, 2011), but higher than on St Eustatius (Caribbean; 59.6%; Madden 2017). St Helena's fledging success (52%) is lower than that in both Mexico and St Eustatius (both 78%). The majority of other Red-billed Tropicbird population studies report much greater overall breeding success than at St Helena (33%) for example, on St Eustatius (48.4% Madden (2017)) and Saba (65%, Boeken (2016)) in the Caribbean, Ascension Island, South Atlantic (52%, Stonehouse (1962)), and Senegal (average 55.1%, Diop *et al.*, (2019)). However, Snow (1965) reported even lower breeding success (32%) on the Caribbean island of Daphne. However, this still places St Helena as having the lowest breeding success rates reported globally for the species.

2.5.4. Causes of breeding failure

Agonistic interactions between adult tropicbirds are not unusual (Schaffner, 1991). Nevertheless, conspecific egg predation was not detected during the study period, although it is known to occur by competing adult Red-billed Tropicbirds in Saba (Terpstra *et al.*, 2015). Similarly, egg predation by rat *Rattus norvegicus* is known to occur to Red-billed Tropicbird eggs in St Eustatius (Madden and Ellis, 2013). In St Helena in 2018, despite the presence of an actively incubating adult, one egg was observed being depredated by a rat from nest camera images (Beard *et al.*, unpubl.). Crabs are also a known common cause of nesting failure e.g., in White-tailed Tropicbirds *Phaethon lepturus* in Puerto Rico (Schaffner, 1991), and Brown Noddies *Anous stolidus* on Egg Island, St Helena (Rowlands *et al.*, 1998). More research on these potential threats and the effectiveness of nest defence behaviours is required to better understand the consequences of predation on Red-billed Tropicbirds.

The devastating negative effects of introduced mammalian predators on small oceanic islands have been well documented, e.g., Courchamp *et al.*, (2003), Hilton and Cuthbert (2010). Feral and domestic cats are known predators of two petrel species occurring on

the mainland of St Helena (Beard, 2016), so it is not surprising that chick predation was the main cause of fledging failure in this present study.

Camera images (Beard *et al.*, unpubl.) showed that two domestic dogs caused four breeding failures, two directly through chick predation and two indirectly through disturbance. Given the more remote location of other Red-billed Tropicbird colonies around St Helena, the close proximity of the monitoring sites to human habitation and the fact that only domestic (not feral) dogs were observed in the colony, the impact of dogs on the entire St Helena population is likely less severe than my results suggest.

There were no incidences of swamping of nests by ants causing breeding failure, unlike observations for other tropicbird populations (e.g., Mejías, Wingate, *et al.*, (2017); Luna *et al.*, (2018)), and other bird species in St Helena (e.g., Burns *et al.*, (2013)). Likewise, there were no observed negative effects of litter e.g., through entanglement or ingestion (Hyrenbach *et al.*, 2013; Vanderwerf and Young, 2014) despite part of the mainland monitoring site encompassing a disused refuse dump.

2.5.5. Replacement clutches

Many bird species will attempt to lay a second clutch within the same breeding period if the first nesting attempt fails. Whether tropicbirds lay a replacement clutch is often dependent on the stage of failure and/or the date that the first attempt failed (Sommerfeld, Stokes and Baker, 2015). Since environmental conditions tend to deteriorate during most seabird breeding seasons (Hamer, Schreiber and Burger, 2002), increased energetic costs can render late-season clutches unsustainable (Mejías, Wiersma, *et al.*, 2017). My findings suggest that, at St Helena this does not translate into lower likelihoods of late-season re-nesting attempts: pairs that laid replacement clutches were observed in relatively equal stages of initial breeding failure (incubation: 46%, chick rearing: 56%). The observed incidence of replacement clutches was relatively low; only 14% of the pairs that initially failed subsequently laid a replacement clutch, compared to 53.1% reported from Red-billed Tropicbirds in the Caribbean (Madden, 2019). Red-billed Tropicbirds at St Helena are able to breed every month of the year. It is therefore possible that they abstain from immediately laying a replacement clutch and return to the colony earlier in the following breeding period to initiate a new breeding attempt, despite evidence that laying replacement clutches did not significantly influence periodicity.

2.5.6. Habitat preferences

This study has identified the type of cavity and the number of entrances as important predictors of cavity occupancy and nest occurrence, but not of reproductive performance. Adult Red-billed Tropicbirds favoured using enclosed cavities, with fewer entrances, such

as a tube types, compared with more open cavity types. The nest chamber volume is the most important predictor in the final model of cavity occupancy, while the number of entrances was the most significant predictor of nest site selection. Inside the nest, the presence of soil rather than harder materials, such as rough volcanic rock positively influenced hatching success, likely reflecting a lower risk of egg damage. The slope of the nest bowl also influences cavity occupancy and fledging outcomes: flatter nest bowls likely help to keep the egg and/or chick on the nest site when adults arrive and leave.

2.5.7. Management implications

The high level of chick predation by mammalian predators identified as the main cause of fledging failure is a cause of concern for the long-term viability of the "Ladder Hill" IBA colony of Red-billed Tropicbirds. The observed high fidelity to nest sites and cavities, continued poor breeding success and disturbance from mammalian predators will likely lead to a reduction in colony size and range, possibly reducing the colony to inaccessible cliff areas. Stricter controls on free-roaming cats and dogs in residential areas near the colony, backed up by suitable legislation, along with improved compliance with existing regulations such as registering, neutering and micro chipping all owned pets (Jensen and Thomsen, 2022), in conjunction with an education and public awareness campaign, would help to reduce the number of cats and dogs foraging within the IBA. Expansion of the existing feral cat control programme for St Helena Plover IBAs should also include the Ladder Hill IBA, along with a feasibility study on constructing an exclusion area around the IBA. Installation of artificial nest chamber "igloos" (see Chapter 3 and Medeiros, (2008)) on accessible offshore islets such as Egg Island could be an important tool to increase cavity availability in predator-free areas.

Chapter 3.

Increasing use of artificial nest chambers by seasonally segregated populations of South Atlantic Storm-petrels (*Hydrobates helena*) at St Helena, South Atlantic Ocean

This chapter has been published in *Marine Ornithology* under the title 'Increasing use of artificial nest chambers by seasonally segregated populations of Band-rumped Storm-petrel (*Hydrobates castro*) at St Helena, South Atlantic Ocean'.

3.1. Abstract

Artificial nest chambers have become a common management tool for monitoring nocturnal burrow-nesting seabirds, although their utility varies among species and locations. The South Atlantic Storm-petrel *Hydrobates helena* is likely a new cryptic species endemic to the south Atlantic. Here I evaluate the installation of artificial nest chambers as a tool for long term conservation and monitoring of this species breeding in two distinct seasons on the same island at St Helena. Based on six years of observational data, I analysed factors affecting occupancy, mate and chamber fidelity, and reproductive success, to optimise nest chamber installation and to enhance their future management. Occupancy rates were high overall, increasing from 5% after the first season following installation to 85% after five years. Occupancy was positively associated with i) the number of seasons since chamber installation, ii) whether the chamber was occupied in the previous season, iii) and in the same season in the previous year. Occupancy also varied with chamber location and lid construction material, wooden lids had 7% lower overall occupancy and 18% lower breeding success than other lid types. Chamber lid replacement also negatively affected occupancy. Chamber monitoring revealed that individuals showed up to 93% mate fidelity and 86% chamber fidelity, with little effect of previous breeding outcome. From 312 monitored nests, hatching success was 15% higher during the hot season, while fledging success was 5% higher during the cool season, leading to only 0.4% difference in overall productivity between seasons. Fledging success of each seasonal population varied by year. Chick mortality was considerably higher during the hot season (41% compared to 13% during the cool season), possibly reflecting differences in temperature regime. I conclude that installation of artificial nest chambers represents an effective monitoring tool, and recommendations for the design and management of chambers are discussed.

3.2. Introduction

Small seabirds that are nocturnally active at the colonies are challenging to monitor due to their secretive nature, spending much of the year out at sea and only returning to land in darkness during the breeding season. Furthermore, seabirds often nest on steep cliffs and/or are restricted to offshore islands which are difficult to access, especially for burrowing and cavity nesting species. The availability of suitable nesting cavities may be a limiting factor for many populations (Bolton *et al.*, 2004) and conservation actions on breeding grounds can be easier to implement, less expensive and more effective than conservation actions at sea (Wilcox and Donlan, 2007). Providing nest boxes or artificial burrows has therefore become a common management tool for monitoring and conservation of different seabird species (Bourgeois, Dromzée and Vidal, 2015), including burrow-nesting seabirds (Bolton *et al.*, 2004).

The breeding success of seabirds in nest boxes has been shown to be generally higher than breeding success in natural sites, mainly due to more effective protection from predators (Libois *et al.*, 2012), reduction in egg damage and inter- or intra-specific interferences (Bolton *et al.*, 2004), while nest site characteristics and degree of competition can also affect breeding success (Warham, 1990). However nest boxes can also potentially have undesirable negative effects on a population by acting as ecological traps (Mänd *et al.*, 2005), through increasing attractiveness to predators (Sanz *et al.*, 2003), reducing breeding success (Rodriguez, Aviles and Parejo, 2011), or long-term survival of fledglings (Klein *et al.*, 2007). The construction materials used can also affect the temperature inside the chamber, which can indirectly impact productivity (Carlile, Priddel and Madeiros, 2012).

Artificial nest chambers have been used for several storm-petrel species (Allan, 1962; Ramos *et al.*, 1997; Bolton *et al.*, 2004), and can facilitate observation as well as provide access to nest chambers that would otherwise be difficult to access without disturbance. Storm-petrels in particular are highly sensitive to disturbance (including handling) at the nest, which can negatively affect reproductive success, site faithfulness and increase the likelihood of divorce (Carey, 2009). At St Helena, *H. helena* usually breed in two discrete periods, over the austral summer and the austral winter (Bennett, Bolton and Hilton, 2009). Given the potential for the South Atlantic population to be a new species, with a restricted range and thus expected to be of conservation concern, artificial nest chambers were installed in an existing colony at St Helena. The aims of this management measure were to (a) provide a convenient way of monitoring the breeding productivity of the two seasonal sub-populations, (b) protect vulnerable nests from disturbance, e.g., from

handling disturbance and from other competing species, (c) increase the availability of suitable nest sites, and (d) improve breeding success.

This study aims to assess the use of artificial nest chambers as a conservation management and monitoring tool for *H. helena*, a potential endemic in the south Atlantic, through presenting data on occupancy levels, fidelity, and breeding success. I analysed factors affecting these parameters in artificial nest chambers to enhance their use for conservation, through improving their installation and thereby future management of the species. I broadly predict a high occupancy level of nest chambers if there is a shortage of nest sites on the island. Given that the sub-population breeding during the hot season is bigger than the breeding population during the cool season (unpublished data), I explored the following hypotheses: 1) The rate of uptake of artificial nest chambers was expected to be higher in the hot season, due to higher inter-specific competition for nesting cavities in this population. 2) The cool season population was expected to have a higher breeding success than the hot season population due to lower disturbance from other breeding seabird species and lower inter- and intra-specific competition. This hypothesis is justified by seasonal differences in breeding success between the two populations observed in natural nesting cavities (Bennett, Bolton and Hilton, 2009). 4) If nest chamber characteristics are adequate for the protection of eggs and chicks, their use is expected to result in a higher breeding success than for those storm-petrels breeding in natural cavities.

3.3. Methods

3.3.1. Study site and species

This study was carried out on Egg Island (15°57'57"S 5°46'39"E, Figure 3.1), a small predator free volcanic island off the north-west coast of St Helena, harbouring the largest sub-population of *H. helena* in the South Atlantic (unpublished data). This study was conducted over six years, encompassed five hot seasons (2014-2018) and five cool seasons (2015-2019). There are two seasons per year; the hot season in the austral summer from late September to late December, and the cool season in the austral winter between late March to early July (Bennett, Bolton and Hilton, 2009). The island is often used by different species overlapping in breeding phenology; other burrow-nesting Procellariiformes known to occur in very small numbers on Egg Island are; Bulwer's Petrel (*Bulweria bulwerii*) (Oppel *et al.*, 2012) and White-faced Storm-petrel (*Pelagodroma marina*) (Bolton *et al.*, 2010). During the hot season, Brown Noddies (*Anous stolidus*) and a small population of Sooty Terns (*Onychoprion fuscatus*) are the only other species that nest on the open slopes near storm-petrel nesting cavities.

3.3.2. Artificial nest chambers

Artificial nest chambers (hereafter "chambers") were installed in early March 2014 ($n = 40$), 2015 ($n = 50$), late February 2017 ($n = 20$) and early April 2018 ($n = 20$). Installation was conducted during the day, when most adults are out at sea (pers. obs.). The chambers were positioned a minimum of two meters away from natural burrows in three areas on the island (Fig. 1c), in locations without previous presence of natural nests to reduce disturbance. All installation locations were in the open, as the island has limited vegetation cover or natural shelter. The chambers were made from PVC, following a simple design described by Bolton *et al.*, (2004), but using two different lid materials; either brown or green PVC or brown plywood (Fig. 2).

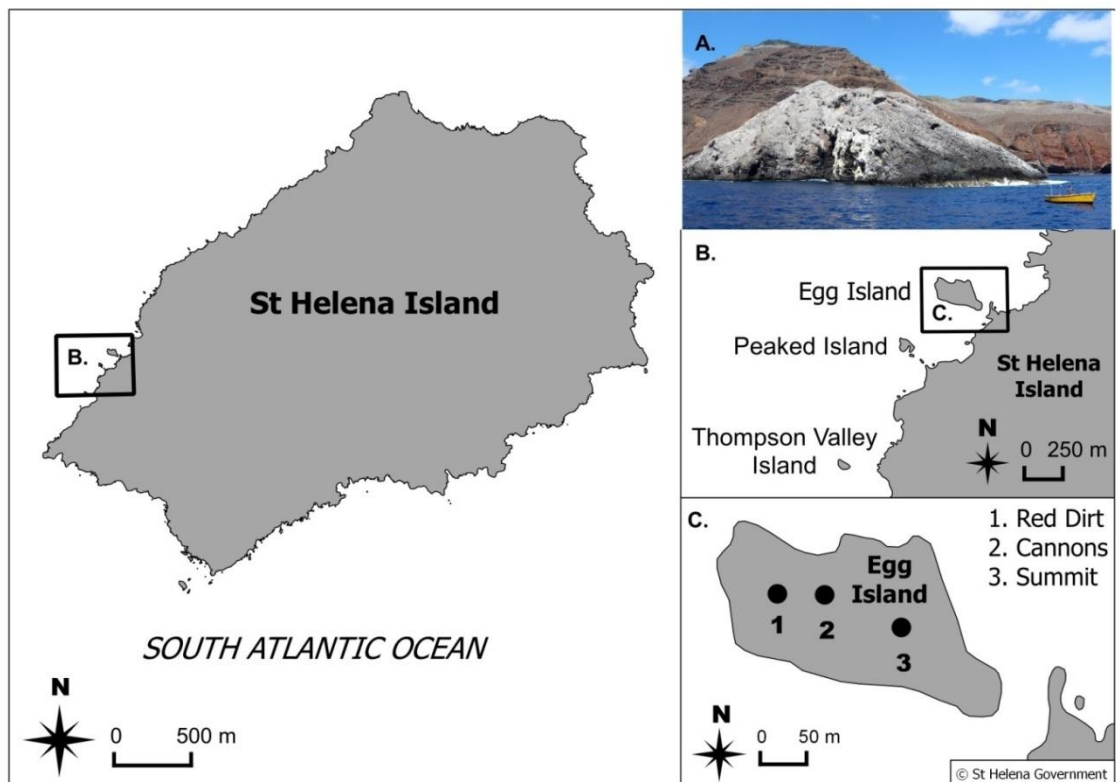


Figure 3.1. Location of the study site at St Helena A) view of Egg Island from the sea (foreground) with St Helena in the background (Photo: St Helena Government). B) Location of Egg Island in relation to other nearby offshore islands. C) The three groupings of artificial nest chamber locations on Egg Island.



Figure 3.2. Artificial nest chambers installed on Egg Island, showing the different lid materials; ply wood (bottom) and PVC (top) (Photo: Annalea Beard).

3.3.3. Monitoring protocols

During each season, chambers were inspected a minimum of four times with a maximum interval of four weeks between visits per season, to determine chamber occupancy and nesting fate. Care was taken to leave the entrance as undisturbed as possible. I considered a chamber to be occupied if an adult was present on at least one occasion during monitoring. All storm-petrels present in a chamber were ringed for subsequent individual identification. If an egg (or adult bird incubating) was present on at least one of the visits it was deemed a nesting attempt. Any chamber lids that were damaged or missing were noted and replaced with the same lid type within the same season. If replacement was not possible due to the lack of available materials the chamber was considered unavailable for the season.

3.3.4. Data analysis

All statistical analyses were carried out in R 4.1.2 (R Development Core Team, 2021). All generalised linear mixed models (GLMMs) were implemented in the *lme4* package (Bates *et al.*, 2015), all general liner models (GLMs) and chi-squared tests in the *stats* package (R Core Team and contributors worldwide, 2021), all likelihood ratio tests (LRTs) in the *lmerTest* package (Zeileis and Hothorn, 2002) and all GAMMs in the *gamm4* package (Wood & Scheipl, 2020) following Thomas *et al.*, (2017). Significant effects ($P < 0.05$) in all final models were plotted using the *ggplot2* R package (Wickham, 2016).

3.3.4.1. Breeding success and productivity

I excluded 15 of the original 327 nesting attempts where either fate or the failure stage could not be ascertained. Three re-nesting attempts following initial breeding failure in a season were pooled in the analysis. For ease of comparison between breeding success and productivity in natural nesting cavities and chambers, I closely followed the methods described by Bennett *et al.*, (2009), which I summarise here: For each season and year, I estimated the daily egg and chick survival rate corrected for the exposure time of nests to account for nests being discovered at various stages (Mayfield, 1975) and reported their standard errors following Johnson (1979). Hatching success and fledging success were calculated assuming a 42 days incubation and 70 days chick development period, respectively (Allan, 1962; M. Harris, 1969). Breeding success, the proportion of eggs laid that result in a fledged chick, were calculated as a product of hatching and fledging success.

I tested for differences in hatching and fledging success between each season, year and within each season between years using logistic exposure models (GLMMs). Logistic exposure models are similar to logistic regression models in that the response variable is binomial (success or failure of nest occurred between nest checks), but the link function is modified from the logit link to consider nest exposure days (Shaffer, 2004). I used chamber ID as a random effect, to account for any environmental stochasticity among the chambers and used a likelihood-ratio test (LRT) (Lewis, Butler and Gilbert, 2011) to compare candidate models to a null model which lacked any covariates. I examined parameter estimates of significant terms to determine the direction of the effect. Comparisons of chick mortality between seasons were made using chi-squared tests.

3.3.4.2. Occupancy

I examined chamber use since installation by calculating the proportion of chambers either occupied or used for breeding out of the number of chambers available for each season after installation. I used GLMMs to assess if occupancy and breeding use was associated with 1) number of seasons since initial installation (installation length), 2) year as a factor (2014-2019), 3) season (hot vs. cool) as independent variables, as well as 4) a two-way interaction (year x season). Both occupancy and breeding use were modelled as binary response variables (occupancy; 1= occupied or 0 = unoccupied, and breeding; 1 = used for breeding or 0 = not used for breeding) with a 'logit' link function and binomial error distribution. Chamber location and identity were treated as nested random effects, to account for repeated measures of the same individual chambers in the same locations. For the analysis of occupancy, I also included additional variables; Previous Season Occupancy (PSO; true/false): whether the chamber was occupied in the previous season (e.g., hot season versus previous cool season and vice versa), Previous Between Season Occupancy (PBSO; true/false): whether the chamber was occupied in the same season

the previous year (e.g., hot season versus previous hot season). For breeding use I included the additional variables: Previous Season Breeding Use (PSBU; true/false): whether the chamber was used for breeding during the previous season, Previous Between Season Breeding Use (PBSBU; true/false): whether the chamber was used for breeding in the same season the previous year, the chamber's breeding outcome in the previous season (PSBO): success: true/false), and the chamber's breeding outcome in the same season the previous year (PBSBO): Success: true/false). For each variable and response variable, I constructed two models: one containing the variable as a fixed effect, and a null model without the variable as an effect. To assess each variable I compared the two models using a LRT (Lewis, Butler and Gilbert, 2011), and determined variables to be a significant predictor of either occupancy or breeding use if the model containing the variable of interest was significantly better than the null model. I then further explored which of the candidate variables best explained occupancy of a chamber, through constructing a global model containing; year, season, year x season, PSO, PBSO, and installation length. Model selection was performed by removing variable that most reduced Akaike's Information Criterion adjusted for the effect of sample size (AICc) to identify the most parsimonious model (Burnham and Anderson, 2002).

3.3.4.3. Chamber fidelity and mate fidelity

I calculated chamber location fidelity, chamber identity fidelity and individual mate fidelity using the ringing data gathered from individuals identified using chambers during the study. The influence of previous breeding failure on chamber fidelity and mate fidelity was assessed by comparing the proportion of nesting attempts where at least one individual from the breeding pair was identified and bred more than once in successive years, versus the equivalent proportion where individuals changed chamber or partner between successive years.

3.3.4.4. Location and Lid

I used a GLM with a binomial distribution and 'log' link function to test the effect of 1) chamber location (summit, cannons or red-rock) and 2) lid type (wood or PVC) on occupancy of chambers and reproductive performance. I first defined A) overall occupancy for each chamber as the ratio of the number of breeding seasons the chamber was used by storm-petrels out of the number of breeding seasons the chamber was available, and B) overall reproductive performance for each chamber as the ratio of the number of successful breeding attempts out of the number of breeding attempts that occurred in the chamber. I weighted these parameters with either the number of seasons the chamber was available, or the total number of breeding attempts, respectively. For this analysis I excluded chambers where the lid had been replaced, as I tested for any effect

of replacing the lid separately. Results from the GLMs were presented using the full models, and predictions from these GLMs were plotted. To examine what effect replacing a lid on a chamber may have on occupancy, I used a subset of chambers which, during the study had lids replaced and excluding any seasons where the lid was absent. I then constructed two binominal GLMMs with 'logit' link function (as above) on the binary response variable (occupancy true/false), with chamber location and identity as nested random effects and installation length (the number of seasons the chamber had been installed) as a fixed factor in both models. One model was run with no explanatory variables (null model) and one with lid present/replaced as an explanatory variable. A LRT between the two models was then used to test whether having the lid replaced in a given breeding season significantly influenced occupancy in that season.

3.4. Results

3.4.1. Nest success and productivity

I obtained reliable data on breeding success from 312 nests; 187 during the cool season and 125 during the hot season (Table 3.1). Mayfield hatching success in chambers during the study was estimated at 47%. Mayfield hatching success during the hot season (pooled across years) was estimated at 55% (95% CI 0.470-0.644) and thus higher than during the cool season (40%, 95% CI 0.330-0.485, LRT $\chi_1^2=6.9247$, $P = 0.009$, $n = 285$, Figure 3.3A). There was no indication that hatching success varied between years (LRT $\chi_1^2 = 0.0173$, $P = 0.895$, $n = 285$) or within each season between years (LRT $\chi_2^2 = 0.0816$, $P = 0.960$, $n = 285$).

Overall fledging success in chambers was estimated by the Mayfield method to be 19%. Fledging success was estimated to be overall five percentage points higher during the cool season (21% estimated fledging success, 95% CI 0.190-0.238) due to higher daily chick survival rates (Table 3.1) than during the hot season, when fledging success was estimated to be 16% (95% CI 0.128-0.203, LRT $\chi_1^2=16.93$, $P < 0.001$, $n = 171$, Figure 3.3B). Fledging success was also significantly different between years when pooled across seasons (LRT $\chi_1^2=13.942$, $P < 0.001$, $n = 171$); 2016 showed the highest daily chick survival rates and fledging success estimates compared to other years. There was also evidence of differences in fledging success within each season between years (LRT $\chi_2^2=28.864$, $P < 0.001$, $n = 171$), the hot season showing lower fledging success across years than the cool season (Table 3.1, Figure 3.4). Productivity overall was estimated to be 9%, with only a 0.4 percentage point difference between seasonal populations (cool season 8.5%, hot season 8.9% productivity respectively).

Table 3.1. Summary of breeding success of *H. helena* nesting in artificial nest chambers on Egg Island from 2014 to 2019. *n* hatched is the number of clutches that hatched, *n* fledged is the number of hatched chicks surviving to fledging.

Year	<i>n</i>	<i>n</i> hatched	Daily nest survival	Hatching success	<i>n</i> fledged	Daily fledging survival	Fledging success	Producti- vity
Hot season								
2014	7	3	0.969 ± 0.015	0.265	3	0.938 ± 0.000	0.011*	0.003
2015	9	4	0.985 ± 0.007	0.520	4	0.951 ± 0.000	0.030*	0.016
2016	27	18	0.987 ± 0.004	0.567	13	0.990 ± 0.002	0.494	0.280
2017	31	16	0.989 ± 0.003	0.623	12	0.976 ± 0.003	0.185	0.115
2018	51	29	0.985 ± 0.003	0.521	9	0.954 ± 0.005	0.036	0.019
Cool season								
2015	16	10	0.987 ± 0.005	0.581	9	0.971 ± 0.004	0.130	0.076
2016	24	17	0.981 ± 0.007	0.456	14	0.991 ± 0.002	0.540	0.246
2017	44	28	0.971 ± 0.007	0.290	27	0.990 ± 0.001	0.480	0.139
2018	48	13	0.968 ± 0.005	0.250	9	0.958 ± 0.002	0.050	0.013
2019	55	33	0.986 ± 0.003	0.543	29	0.955 ± 0.003	0.041	0.022

* Mayfield fledging success underestimated in 2014 and 2015 hot season as all chicks survived to fledge.

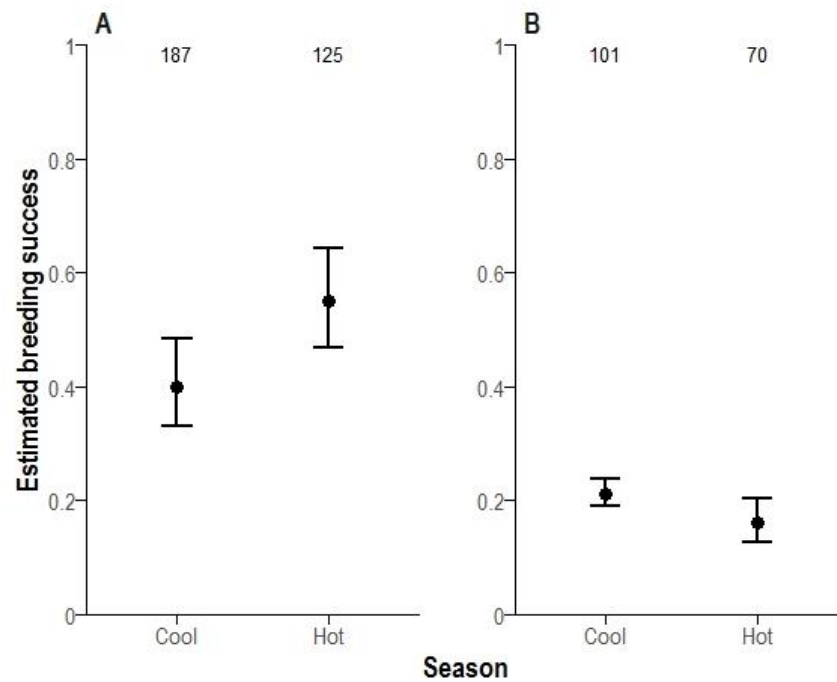


Figure 3.3. Mayfield estimates of nesting success for two seasonal populations of *H. helena* breeding in artificial nest chambers on Egg Island. A) hatching success and B) fledging success. Error bars represent 95% confidence intervals. Sample sizes are indicated at the top.

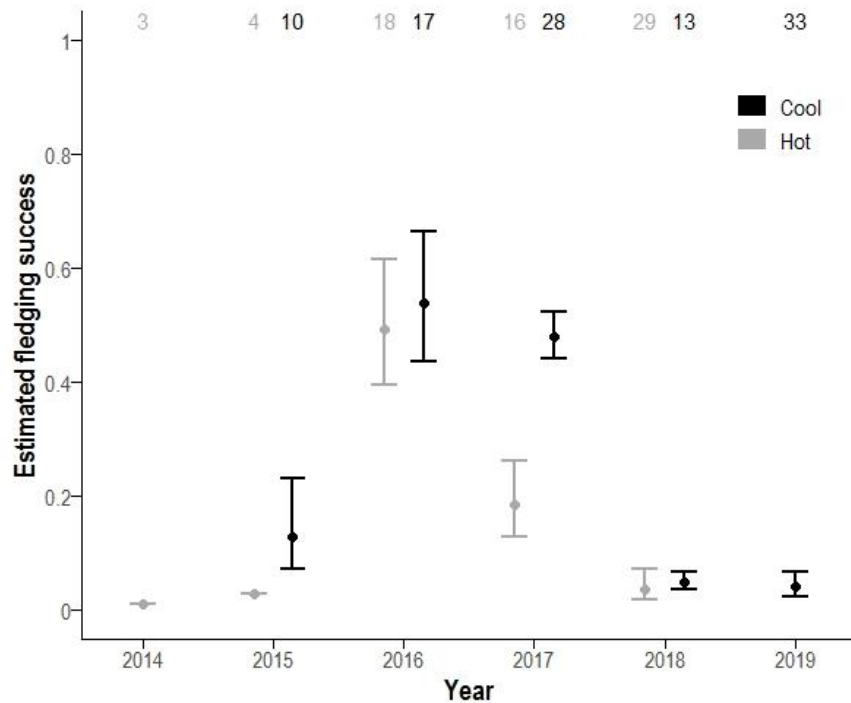


Figure 3.4. Annual Mayfield estimates of fledging success for *H. helena* breeding in artificial nest chambers on Egg Island for each season (hot season: grey; cool season: black). Error bars represent 95% confidence interval. Sample sizes are indicated at the top.

3.4.2. Causes of breeding failure

The cause of hatching failure (pooled across years) was undetermined for 104 of 285 eggs monitored (36.5% of nests), where the egg disappeared from the chamber with no obvious signs of nest disturbance. Seventeen hatching failures (6.0%) were due to the egg being abandoned after initially being incubated. Egg damage caused by stones in the nest chamber floor cracking and breaking the shell accounted for 11 hatching failures (3.9%). A further three losses (1% of nests) were due to an usurper event, where the egg from an active nest was evicted from the chamber and subsequently a different pair started a new nesting attempt. Two losses (0.7%) were due to an apparent absence of incubation; an egg was laid but no adults were ever observed incubating. There was one incidence of a breeding adult dying in a chamber, resulting in hatching failure, and one chick died during hatching when it failed to emerge fully from the egg shell. The cause of fledging failure was undetermined for 41 of 171 (24%) chicks monitored, where the chick died in a chamber with no apparent cause. Observed chick mortality was significantly higher (29 of 70 chicks (41%) failed to fledge) during the hot season (pooled across seasons) than in the cold season (13 of 101 chicks (13%), $\chi^2 = 9.6116$, $P = 0.002$). Only one chick disappeared from a chamber with no signs of disturbance and the cause of one nestling failure was unknown.

3.4.3. Occupancy

Chambers on Egg Island were readily accepted by *H. helena*. 71% (92 of 130) of all installed chambers were occupied at least once during the study, 89% ($n = 82$) of which were used at least once for breeding. In the 2015 and 2017 cool seasons, all occupied chambers were used for breeding. Occupancy and use for breeding both increased with time since the chamber had been installed (occupancy LRT; $\chi^2 = 243.11$, $P < 0.001$, $n = 1050$, breeding LRT; $\chi^2 = 128.39$, $P < 0.001$, $n = 920$). *H. helena* occupied 5.4% of chambers during the first season following installation which increased to 85.0% after five years (10 seasons). Similarly, 4.6% of chambers were used for breeding after the first season following installation, reaching 72.5% after five years (Figure 5).

Chamber occupancy also increased throughout the study period (1.399 ± 0.125 , $z = 11.21$, $P < 0.001$, $R^{2m} = 0.171$, $R^{2c} = 0.713$, $R^{2m} = 0.713$, LRT; $\chi^2 = 190.41$, $P < 0.001$, $n = 1050$). Although chamber occupancy was marginally higher in the hot season (38.48%) than the cool season (36.61%), the difference was not significant ($R^{2m} = <0.001$, $R^{2c} = 0.426$, $z = 0.502$, $P = 0.616$, LRT; $\chi^2 = 0.242$, $P = 0.622$, $n = 1050$). Chamber use in the previous season was positively related to current occupancy (1.958 ± 0.212 , $z = 9.225$, $P < 0.001$, $R^{2m} = 0.171$, $R^{2c} = 0.353$, LRT; $\chi^2 = 83.874$, $P < 0.001$, $n = 920$) as was

occupancy in the same season of the previous year (1.846 ± 0.237 , $z = 7.776$, $P < 0.001$, $R^{2m} = 0.137$, $R^{2c} = 0.397$, LRT; $\chi^2_1 = 60.192$, $P < 0.001$, $n = 787$).

After accounting for repeated observations of each location and chamber, the model that best explained whether a chamber was occupied or not in any given season (Table 3.2A) included the number of seasons that the chamber had been installed for, whether the chamber had been occupied in the same season the previous year, and whether the chamber had been occupied in the previous season ($R^{2m} = 0.394$, $R^{2c} = 0.402$, Table 3.2B, Figure 3.6).

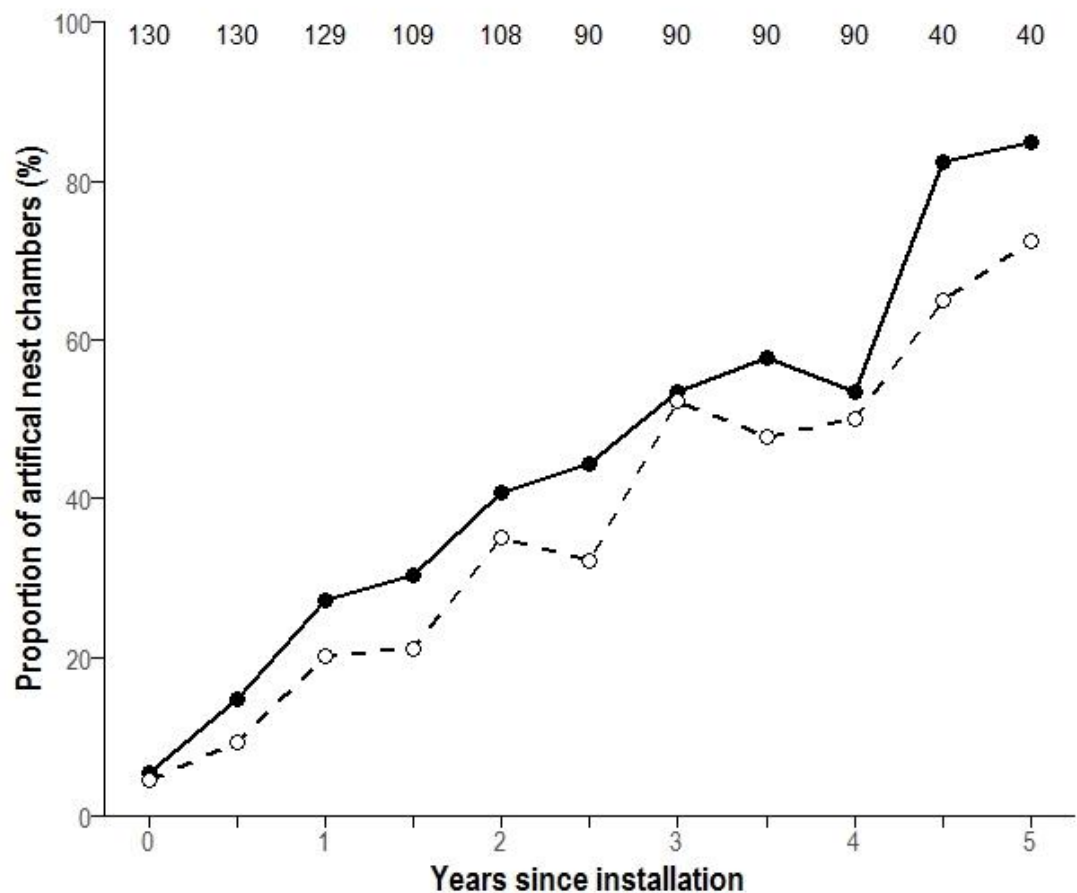


Figure 3.5. Proportion of artificial nest chambers occupied (black points, solid line) and used for breeding (white points, dashed line) by *H. helena* on Egg Island in relation to the number of years since their installation. Numbers at the top indicate the number of artificial nest chambers available for a given number of years.

Table 3.2. A) Competing generalized linear mixed models (GLMMs) assessing which variables were associated with storm-petrel occupancy of an artificial nest chambers on Egg Island between 2014-2019, using chamber location and identification (LOC/ANC ID) as nested random effects; **B)** parameter estimates of variables in the most parsimonious model.

A. Competing models						
Model	Random effects	<i>k</i>	AICc	Delta AIC	AICcWt	Cum.Wt
(4) - Year	LOC/ANC ID	6	796.24	0.00	0.48	0.48
(3) - Year x Season	LOC/ANC ID	7	797.50	1.26	0.26	0.73
(2) - Season	LOC/ANC ID	8	798.07	1.82	0.19	0.93
(1) Global ^a	LOC/ANC ID	9	799.95	3.71	0.07	1.00
B. Significance of variables in model 3						
Variable	estimate	std error	<i>z</i>	<i>P</i> value		
PSO	1.698	0.194	8.751	<0.001		
PBSO	1.599	0.219	7.283	<0.001		
Installation length	0.070	0.041	1.721	0.085		

^a The global model contains all variables (year, season, year x season, previous seasons occupancy (PSO), previous between season occupancy (PBSO), and installation length), other models denote the interaction term that is removed from the global model and the change in AICc this produced. Model selection is based on AICc.

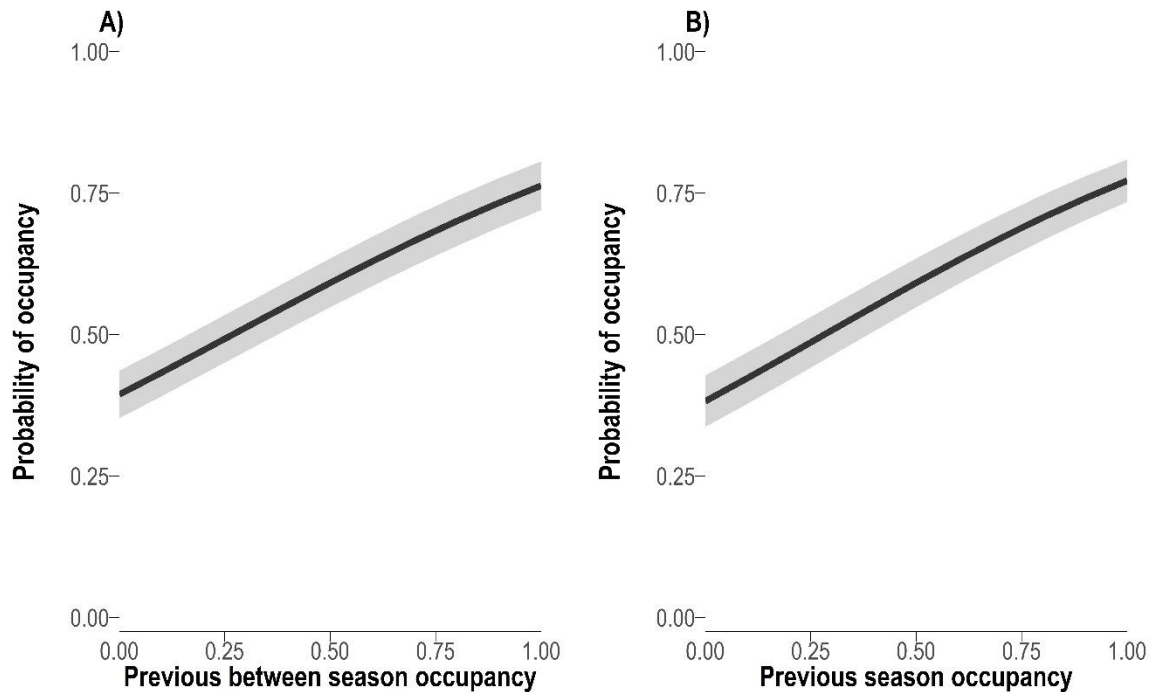


Figure 3.6. Probability of a chamber being occupied with respect to **A)** the occupancy in the same season of the previous year (e.g., cold season vs. previous cold season), and **B)** occupancy in the previous season (e.g., cold season vs. hot). Solid lines represent model predictions based on the most parsimonious model for occupancy (Table 3.2, model 3), using mean values in each model for installation length (4.06 seasons) and in plot A, mean previous season occupancy (0.5), and in plot B), mean between season occupancy (0.5). Shaded areas around the fitted lines represent $\pm$ one standard error (SE).

3.4.4. Chamber use for breeding

The use of chambers for breeding increased significantly across the study period (1.212 ± 0.116 , $R^{2m} = 0.147$, $R^{2c} = 0.670$, $z = 10.47$, $P < 0.001$, LRT; $\chi_1^2 = 152.35$, $P < 0.001$, $n = 1050$). The number of chambers that were used for breeding were only marginally lower in the hot (29.91%) than in the cool seasons (32.37%), but not significantly so ($R^{2m} = 0.003$, $R^{2c} = 0.418$, $z = -1.668$, $p = 0.095$, LRT; $\chi_1^2 = 2.803$, $P = 0.094$, $n = 1050$). The likelihood of chambers being used for breeding was positively related to the previous seasons breeding activity (1.846 ± 0.237 , $z = 7.776$, $P < 0.001$, $R^{2m} = 0.150$, $R^{2c} = 0.299$, LRT; $\chi_1^2 = 73.288$, $P < 0.001$, $n = 920$) and the breeding activity in the same season of the previous year (1.656 ± 0.233 , $R^{2m} = 0.109$, $R^{2c} = 0.342$, $z = 7.094$, $P < 0.001$, LRT; $\chi_1^2 = 49.646$, $P < 0.001$, $n = 787$). However, the breeding outcome in the same season of the previous year (success; true/false) was not related to whether a chamber was used for

breeding in the following corresponding season (LRT; $\chi^2_1 = 0.928$, $P = 0.335$, $n = 206$). Likewise, the previous season's breeding outcome was not related to the use of the chamber in the following breeding season (LRT; $\chi^2_1 = 0.007$, $P = 0.931$, $n = 255$).

3.4.5. Site and chamber fidelity

In total, 302 adults were identified using chambers over the study, 254 (83.3%) of which were using the chamber to breed. There was no overlap in individuals observed between seasons, i.e., no individuals found during the hot season were recorded subsequently in the cool season, and *vice-versa*. 50% (153) of identified individuals used the same chamber in more than one season and 62% (57) of used chambers were occupied by the same individual more than once. Of the 11 individuals recorded in all five years when chambers were used, four were recorded breeding in each season. 55.5% (15) of the 27 individuals recorded in four years were also breeding, 69.1% (29) of the 42 individuals bred in all three years they were recorded, 64.4% (65) of 101 individuals bred in all two years recorded. Of the 121 individuals recorded using a chamber in only one year, 70.3% (85) were breeding.

Individuals showed strong site and chamber fidelity. Overall, 181 of 238 individuals (76.1%) that used a chamber for either roosting or breeding in successive years also chose the same chamber. 55 of 57 individuals (96.5%) that chose to use a different chamber during the study chose chambers at the same overall location (Figure 3.1C) within close proximity (<2 m) to the original chamber. Two individuals that were found roosting in a different chamber at a different chamber location were both using the nearest chamber location (red dirt, cannons or summit) to the previous location at which they had been recorded. Eight breeding individuals changed chambers more than once: four individuals that reverted back to the original chamber where they were initially breeding, and four additional individuals that subsequently chose to change to a different chamber again, but always within the same location (red dirt, cannons or summit) and in close proximity to the other chambers they were recorded using. Of the breeding attempts where at least one partner was identified and bred more than once in successive years, 153 of 187 individuals (81.82%) were faithful to their chamber: 60 of 70 individuals (85.71%) after breeding successfully in the previous year, 82 of 106 individuals (77.36%) after breeding failure (Figure 3.7A). Eleven chamber-faithful individuals had an unknown previous breeding outcome.

3.4.6. Mate fidelity

194 of 327 nesting attempts in chambers (56.6%) had both partners identified. Overall, 89.4% (143/160) of individuals from pairs who were found to nest more than once were identified as being faithful to their mate: 88.1% (126/143) of individuals who were faithful

to their mate were also faithful to the same chamber, while the remaining 11.9% (17/143) nested in a different chamber. 13 of 17 individuals (76.5%) that were not faithful to their mate also chose a different chamber and the remaining four individuals (23.5%) were faithful to their original chamber. Of the breeding attempts where both partners were identified in successive years and had at least one partner nest more than once, overall, 110 of 120 individuals (92.4%) were faithful to their mate: 64 of 70 individuals (91.4%) after breeding failure, 38 of 41 individuals (92.7%) after breeding successfully in the previous year (Figure 3.7B) and eight mate faithful individuals had an unknown previous breeding outcome. Seven of the ten individuals that were not faithful to their mate swapped mates after a breeding failure and three after a successful breeding attempt. I also found two incidences of temporary divorce where one of the mates breeding with a new partner chose to pair with its previous partner during the next breeding attempt.

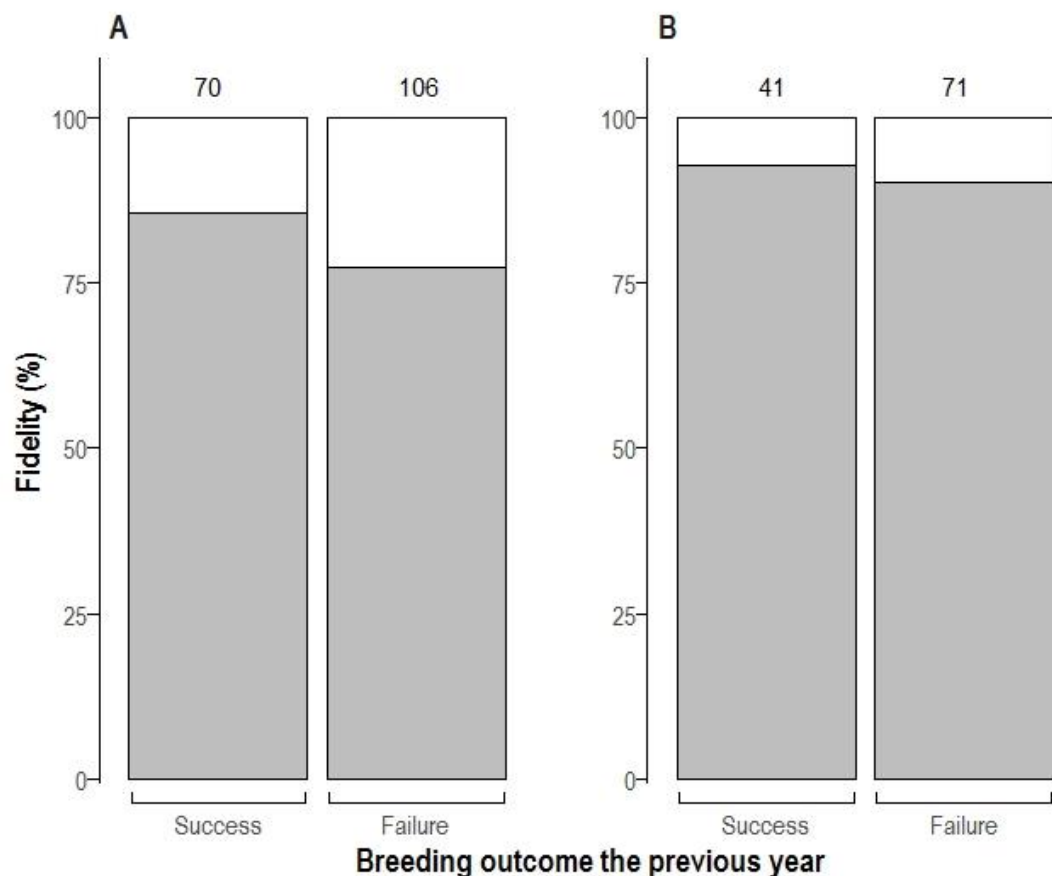


Figure 3.7. Relationship between breeding outcome during the previous season and A) chamber fidelity and B) mate fidelity. Grey indicates fidelity, white indicates non-fidelity. Sample sizes are shown at the top.

3.4.7. Chamber lids and location

Chambers located at the cannons and red rock had a higher overall occupancy than chambers at the summit (0.511 ± 0.143 , $t = 3.564$, $P < 0.001$ and 0.168 ± 0.086 , $t = 1.966$, $P = 0.049$ respectively, $R^2 = 0.018$, Figure 3.8A), however breeding performance did not significantly differ between chamber locations ($R^2 = <0.001$, $X_2^2 = 0.088$, $P = 0.957$). Nine chambers had to have their lids replaced during the study, two of which were replaced twice. Occupancy in those chambers was significantly lower ($-31.3 \pm 10.8\%$) in seasons during which the lid was replaced (LRT; $\chi_1^2 = 11.512$, $P < 0.001$, $n = 79$), compared with chambers which had their lids continuously present during a season. Chambers with wooden and green plastic lids had a considerably lower occupancy than chambers with brown plastic lids (-0.951 ± 0.158 , $t = -6.026$, $P < 0.001$ and -0.278 ± 0.130 , $t = -2.134$, $P < 0.05$ respectively; $R^2 = 0.140$, Figure 3.8B). Chambers with wooden lids also had lower overall reproductive performance than chambers with brown PVC lids, equating to an approximately 18% lower breeding success (-0.774 ± 0.339 , $t = -2.281$, $P = 0.022$; $R^2 = 0.066$, Figure 3.8C), but green PVC lids only had a marginally lower average reproductive performance than brown PVC lids (-0.611 ± 0.334 , $t = -1.826$, $P = 0.069$).

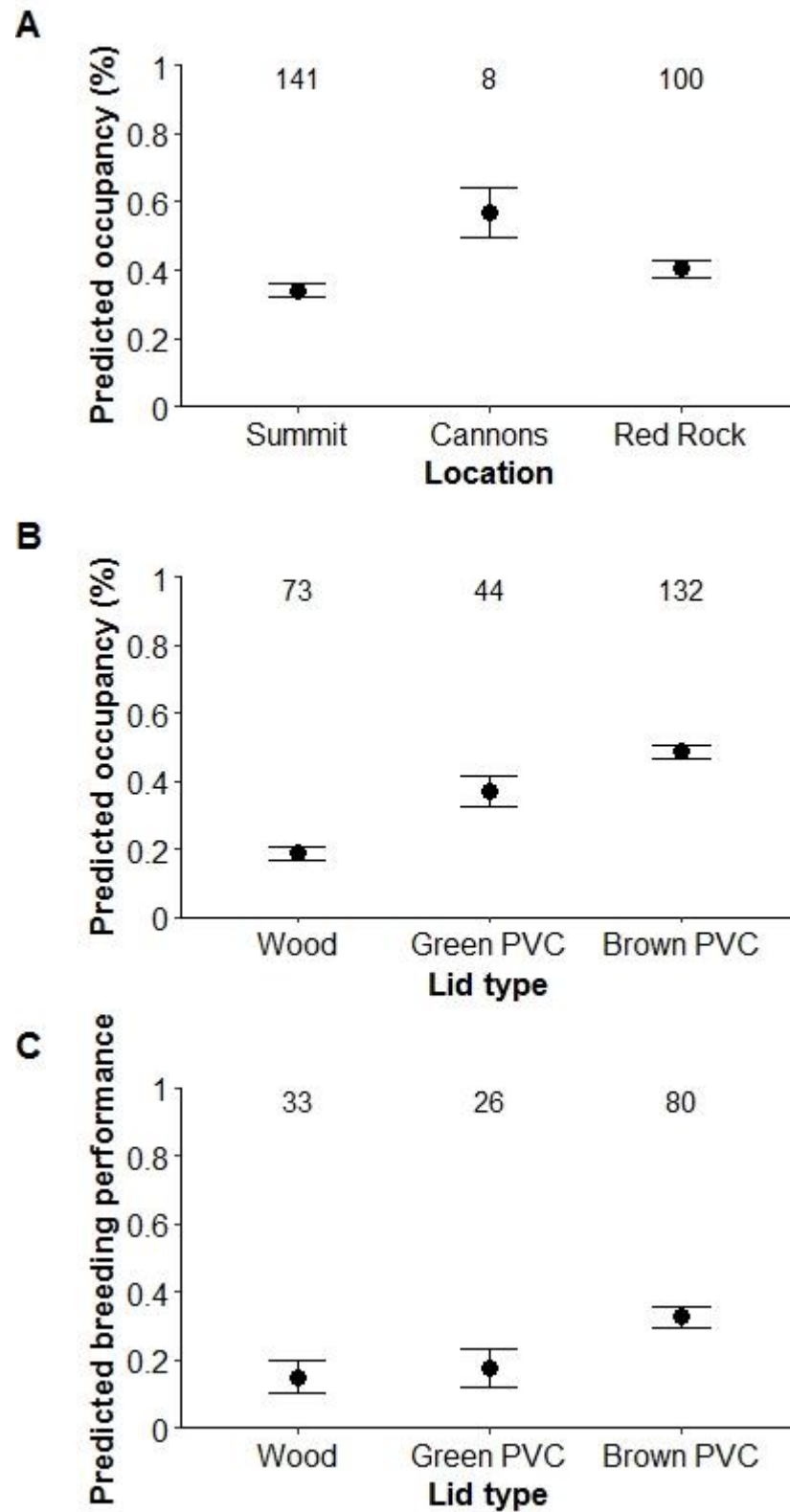


Figure 3.8. Predicted effects of chamber location on A) overall occupancy, B) lid type on overall occupancy and C) lid type on breeding performance. Values represent predicted occupancy and breeding performance $\pm$ 1SE.

3.5. Discussion

I show that artificial nest chambers offer an effective and convenient tool to monitor the breeding biology of burrow-nesting seabirds, and that occupancy of artificial nest chambers increases over time after their first installation. I also show that the two seasonal populations of the South Atlantic Storm-petrel *H. helena* have very similar breeding performances. No apparent exchange or overlap of individuals among seasons were recorded, supporting the placement of St Helena Storm-petrel seasonal populations somewhere on the spectrum of other sympatric but temporally isolated storm-petrel populations where allochronic speciation is underway (Bolton *et al.*, 2008; Taylor *et al.*, 2019).

3.5.1. Reproductive performance

I found significant seasonal differences in success at different breeding stages suggesting that different pressures exist during the incubation and chick rearing period between the hot and cool seasons. My results can be compared with those by Bennett *et al.*, (2009) who studied *H. helena* natural nest cavities at the same study site, although their monitoring period was shorter and in an earlier series of years (2004-2007) than my study. Mayfield estimates for hatching success by Bennett *et al.*, (2009) ranged between 18-43%, lower than the Mayfield estimates of hatching success observed in chambers during my study (25-62%). Fledging success in natural nesting cavities from Bennett *et al.* (2009) study also ranged from 1-67% compared to the marginally lower 1-54% fledging success observed in chambers. Overall breeding success showed similar ranges; <1-27% in natural nest cavities and <1-28% in chambers. These comparisons show both the hot and cool seasonal populations of *H. helena* have considerable variation in success at all breeding stages (hatching, fledging and overall productivity) between years, as is typical for marine seabirds (Schreiber and Burger, 2001). Given the differences in study periods and the observed variation between years, it is impossible to say conclusively that chambers provided higher nesting success and productivity than natural cavities. However, it is encouraging that birds breeding in chambers have so far performed better than or equal to those breeding in natural cavities.

3.5.2. Occupancy

Chambers were occupied and used for breeding within the first season after installation, supporting either their preferential uptake, or that there is a shortage of suitable nesting cavities on Egg Island. This is a fast uptake in comparison to equivalent studies of other storm-petrel breeding populations, in which it could take three or more years to colonise new areas with additional methods such as acoustic attraction (Cruz and Cruz, 1996) and/or chick translocations needed in conjunction to chamber provisioning for successful

establishment (Miskelly and Taylor, 2004). Occupancy was only marginally higher in the hot than in the cool seasons, but fewer chambers were subsequently used for breeding than in the cool season. Altogether this suggests that there may be more non-breeding storm-petrels present during the hot than the cool season. The lower breeding occupancy in the hot season contradicts the hypothesis that there would be higher interspecific competition for nesting cavities during the hot season due to the larger population size. My results indicate that there is little (if any) difference between seasons in the strength of competition for nesting chambers.

The significant positive influence of occupancy in the previous breeding season on the likelihood of chamber use is intriguing. It suggests that there are similarities between the seasons in what attracts storm-petrels to use chambers. It could be pure random chance that storm-petrels in both seasons chose the same chambers, possibly due to having the same habitat preferences. However the important role that olfaction plays in navigation to colony sites and nesting burrows in many petrel species has long been established, with individuals even being able to recognise the olfactory signature of their own nest and mate (Bonadonna, 2009). Findings by Bonadonna and Bretagnolle (2002) showed that diurnal petrel species rely more on visual cues than olfactory cues, whereas nocturnal petrels returning to their nest sites in darkness rely on sense of smell to find burrows. If *H. helena* at St Helena are truly nocturnal, similar olfactory cues might be used by the two seasonal populations, which would explain the influence of between season occupancy on chamber use. Of course, it cannot be disregarded that other influences on chamber choice (e.g., habitat quality around chamber locations, chamber quality, internal environment etc.) may influence occupancy. Although this study found no evidence of overlap in occurrence at the colony between the two seasonal populations (e.g., breeding hot season storm-petrels found on the colony during the cool season and *vice versa*), it may still occur and could further help to explain the influence of the previous breeding season on the likelihood of chamber use.

The significant negative effect of replacing a chamber lid on occupancy within a season was not surprising, given that Procellariiformes are well known for their acute olfactory senses (Bonadonna *et al.*, 2003). This implies that storm-petrels may not recognise their own chamber due to the difference in smell when returning to the colony the following season and/or find the change in odour of a new lid a repellent, preferring to use a nearby chamber instead.

3.5.3. Fidelity

This study provides the first empirical evidence of high levels of both chamber and mate fidelity in *H. helena*, despite inherent limitations in the data. For example, not all of the

individuals that were identified in more than one season were breeding in the same chamber as previously, or identified in the subsequent season. It is therefore not known whether those individuals died/emigrated, chose to nest in a natural cavity, skipped breeding in one or more cycles, or monitoring visits were not frequent enough to detect nesting attempts. Likewise, individuals that were only identified once during the study could have died or moved between sub populations. Contrary to common behaviour among petrels (Bried and Jouventin, 1999; Mariné and Cadiou, 2019), storm-petrels in my research did not necessarily switch nest chamber or overall chamber location following nest failure. Although there was a slight negative effect of previous breeding failure on mate and chamber fidelity (Figure 3.4), chamber use for breeding was unaffected and > 70% of failed individuals still bred in the same chamber. My results indicate that individuals may be more likely to change their chamber following breeding failure the previous season than to change their mate, suggesting that the benefits of maintaining a pair bond may outweigh the cost of pair bond disruption in *H. helena*, even after breeding failure. Mate fidelity is common in Procellariiformes (Warham, 1990), a strategy thought to avoid potentially missing breeding seasons owing to disruption of pair and re-mating, and an initial decrease in reproductive performance with the new mate (Bried and Jouventin, 2002).

Although it was not possible in this study to ascertain an individual's level of breeding experience, it is known to influence mate faithfulness; experienced breeders generally have better breeding success than inexperienced breeders, and in turn unsuccessful breeders in some species are more likely to change their mates (Bradley *et al.*, 1990; H Weimerskirch, 1990; Naves, Monnat and Cam, 2006). Mate fidelity can also sometimes be dependent on site fidelity in some Procellariiformes e.g., Cory's shearwater (*Calonectris borealis*) (Thibault, 1994) but in others species such as Leach's Storm-petrel (*Hydrobates leucorhous*) mate and site fidelity are not necessarily related (Morse and Kress, 1984). It is unclear from this study if mate fidelity is a by-product of site fidelity, or whether site fidelity is a strategy to maintain pair bonds. Site fidelity can serve as a meeting point for pairs to reunite (Morse and Kress, 1984). If there is high competition for nest sites, as suggested by the high occupancy rate observed early after installation on Egg Island, site fidelity may ensure success in the face of strong competition posing the risk of usurpation. Site fidelity also allows individuals to be more efficient at finding a new mate, as they have better knowledge of potential mates in the area (Bried and Jouventin, 2002). The very limited movement observed in this study between overall chamber locations whilst not breeding and restricted 'dispersal' between chambers whilst breeding has also been documented in other seabirds (González-Solís, Wendeln and Becker,

1999), supporting the theory that an individual's knowledge of the surrounding site may influence its choice of site and nest (chamber).

3.5.4. Causes of failure

Egg neglect is common in storm-petrels (Boersma and Wheelwright, 1979), and may have occurred during the study, thus explaining several failures during the incubation period. Monitoring was conducted during the day when adults are most likely to be out to sea foraging and the periodical nature of checks also implies that the timing of nest checks may not have coincided with the presence of the adults. Another potential cause of egg failure is heat stress, which in exposed artificial chambers is known to be a significant cause of death in grey-faced petrel (*Pterodroma macroptera*) chicks in New Zealand (Miskelly *et al.*, 2009). Differences in temperature regulation could therefore account for varying chick survival between seasons, given that air temperatures at St Helena during the cool season range from 16-18 °C, whereas the temperature in the hot season is more variable, ranging from 16-21 °C (Feistel, Hagen and Grant, 2003). It may be more difficult for the parents and/or chick to regulate the temperature of the chick in the chamber during the hot season, potentially augmenting chick mortality. I found the construction material of the chamber lids to influence reproductive performance. Whilst the colour of plastic lids did not significantly impact overall reproductive performance, wooden lids reduced nest success. This could be a consequence of the thermal properties of wood versus plastic, given that the type of construction material used for artificial burrows is known to affect temperatures inside (Carlile, Priddel and Madeiros, 2012). It could also be related to the differences in how the flat wooden lids fit on top of the chamber compared to the plastic lids which have an overlapping edge. Regardless, the lid is the most exposed part of the chamber to direct sunlight and inclement weather, rendering it plausible that this component of chambers may be particularly relevant to breeding success in the chambers.

As expected, there was little evidence of inter-specific competition within the chambers during the study, although the hot season coincides with the brown noddies breeding season. Brown noddy chicks were frequently found blocking chamber entrances, presumably seeking shelter from direct sunlight during the hot season. Small noddy chicks were also observed inside the chamber with incubating storm-petrels or storm-petrel chicks (Figure 3.9). This could influence the ability of parent storm-petrels to attend to the nest, feeding frequency of chicks, and ultimately nesting outcome.



Figure 3.9. Artificial nest chamber with large downy storm-petrel chick (top) and downy with feathers Brown Noddy (*Anous stolidus*) (bottom) sheltering inside found during routine monitoring at the end of the 2016 hot season on Egg Island (Photo: Annalea Beard).

This study could not attribute any causes of breeding failure to predation. Although Egg Island is indeed currently free from invasive feral cats, rats and mice, other resident species may cause predation. For example, Ascension Sally Lightfoot Crabs (*Grapsus adscensionis*) commonly predate bird eggs, causing clutch failure in brown noddies (*Anous stolidus*) on Egg Island (Rowlands *et al.*, 1998). Storm-petrel eggs may likewise be targeted, if accessible. Furthermore, Common Mynas (*Acridotheres tristis*) were frequently observed around the colony during monitoring and seen to enter nesting cavities (pers. obs.). Whilst mynas are a significant predator of endemic St Helena Plover (*Charadrius sanctaehelenae*) eggs (Burns *et al.*, 2013), I did not observe any clear evidence of egg predation. Invertebrate predation of storm-petrel eggs and chicks is also conceivable. Centipedes were found to predate Black Winged Petrel chicks (*Pterodroma nigripennis*) specifically targeting the hind neck, on Phillip Island in the South Pacific (Halpin *et al.*, 2021). Red-headed Centipedes (*Scolopendra morsitans*) were often seen hunting at night in the open on Egg Island, and some storm-petrel chicks were observed with damage to the head and neck (pers. obs.) during this study. Similar damage to storm-petrel chicks have been observed in the Azores (H. Hereward pers. comm.) and on Ascension Island, where Allan (1962) referred to scars and the absence of down on the head as "mohawks", attributing the damage to low ceilings of certain natural chambers and/or other petrels. Therefore, such damage to chicks is more likely to have occurred from interspecific competition with other pairs trying to evict a chick from its chamber rather than caused by centipedes. In addition, ants are known to predate St Helena Plover nests (Burns *et al.*, 2013) and have been observed swamping Fairy Tern (*Gygis alba*) chicks (A. Beard pers obs.), although predation by ants is uncommon they consequently could also affect storm-petrels.

3.5.5. Management implications

The range of hatching and fledging success as well as overall productivity observed in artificial nest chambers (this study) compared with natural nest cavities monitored ten years previously on St Helena (Bennett, Bolton and Hilton, 2009), suggests that chamber provisioning on Egg Island does not reduce storm-petrel productivity or constitute an ecological trap. This is further supported by the high occupancy rate observed early after installation, suggesting that storm-petrels on Egg Island have a shortage of available nest sites. It would be advantageous for future monitoring to include a subset of natural nests to be monitored simultaneously with chambers for a more detailed analysis of differences in productivity between natural versus artificial nesting attempts and variations between years. I tentatively conclude that provisioning of artificial nest chambers is an effective conservation management tool for storm-petrels at St Helena, providing easy access for monitoring breeding productivity and increasing the availability of suitable nest sites.

Reinforcement of current bio-security protocols would be beneficial to ensure that new potentially harmful invasive species do not become established on the island. It may be prudent to include as part of the routine monitoring programme additional invasive species checks to enable detection of new invasions (especially mammals), to ensure that the island remains predator free. Given the observed negative effect on occupancy of replacing a chamber lid, it would be sensible to ensure that protocols are adhered to during monitoring checks. This could include verification that lids have been secured to the chamber adequately upon completion of the monitoring of each chamber location, reducing the risk of lids being lost, e.g., from strong winds. It would also be advantageous to investigate other methods of securing lids to chambers in the long term. If lids are lost or new chambers are installed, then lids (replacements or otherwise) should be ideally constructed of PVC, preferably brown in colour, as I found those to be associated with significantly higher overall occupancy and breeding performance compared with other lid types. Future chamber installations should carefully consider choice of site location. On Egg Island, preference should be given to canyons, red rock and summit respectively, although it is recognised there may be limitations in availability of suitable areas at each site for installation. Other small islands nearby known to contain seasonally breeding *H. helena*, e.g., Peaked Island and Thompson Valley Island, may also be options for future chamber installation. To reduce the risk of egg breakages, installation of new or replacement chambers should ensure that the material used to pack the inside of the nest chambers follows Bolton *et al.*, (2004) guidance; gravel at the bottom to facilitate drainage, topped with soil or small stones. Finally, it may be helpful to provide larger shelters using natural stone near storm-petrel nest chambers located in brown noddies colonies, to mitigate against disturbance from noddy chicks during the hot season.

Chapter 4.

Between-year and spatial variation in body condition across the breeding cycle in a pelagic seabird, the Red-billed Tropicbird

This chapter has been published under the same title in *Ecology and Evolution*.

4.1. Abstract

Body condition in pelagic seabirds impacts key fitness-related traits such as reproductive performance and breeding frequency. Regulation of body condition can be especially important for species with long incubation periods and long individual incubation shifts between foraging trips. I show that body condition of adult Red-billed Tropicbirds (*Phaethon aethereus*) at St Helena Island, South Atlantic Ocean, exhibited considerable variation between years (2013-2017) and between different stages of the breeding cycle. Females took the first incubation shift following egg laying, after which males and females alternated incubation shifts of varying length, ranging from <1 to 12 days. Body condition declined in both sexes during the incubation shift by an average of 22g (2.83% of starting mass) per day and over the incubation period; mass loss was significantly greater during longer incubation shifts, later within a shift and later in the total incubation period. There was also significant differences in incubation behaviour and body condition between years; in 2015, coinciding with a moderate coastal warming event along the Angolan-Namibian coastlines, adults on average undertook longer incubation shifts than in other years and had lower body condition. This suggests that substantial between-year fluctuations in the Angola Benguela upwelling system may influence prey availability, in turn affecting incubation behaviour and regulation of body condition. Adults rearing chicks showed a significant reduction in body condition when chicks showed the fastest rate of growth. Chick growth rates during 2017 from two localities in the Atlantic Ocean: an oceanic (St Helena) versus neritic (Cabo Verde) population were similar, but chicks from St Helena were overall heavier and larger at fledging. Results from this multi-year study highlight that flexibility and adaptability in body condition regulation will be important for populations of threatened species to optimise resources as global climate change increasingly influences prey availability.

4.2. Introduction

Body condition in birds is a key factor underlying the success of breeding, migration and moult. In seabirds, parental body condition is known to influence and impact breeding and

foraging regimes (Fisher, 1967; Quillfeldt, Masello and Hamer, 2004; Labocha and Hayes, 2012). In pelagic seabirds, spending much of their time at sea and only returning to land to breed, it is challenging to understand the pressures acting upon them, such as the energetic costs of breeding and how they respond to these costs. Whilst body condition and its regulation in Procellariiformes (albatrosses, petrels and shearwaters) and Sphenisciformes (penguins) have been examined in detail, for example (Croxall, 1982; Croxall and Ricketts, 1983; Henri Weimerskirch, 1990; Chastel, Weimerskirch and Jouventin, 1995; Clay *et al.*, 2023), Phaethontiformes (tropicbirds) have so far received little attention in this respect (Le Corre *et al.*, 2003).

In seabirds, the division of breeding duties can influence breeding success. Males and females generally share the breeding duties equally (Croxall and Ricketts, 1983), but differing parental investment between the sexes while breeding can occur in some species (Phillips, 1987; Chaurand and Weimerskirch, 1994; Weimerskirch, 1995; Pinet *et al.*, 2012). Differences between sexes in breeding behaviour and regulation of body condition have been attributed to sexual size dimorphism (Lormée *et al.*, 2003; Weimerskirch *et al.*, 2006). Tropicbirds are typically monomorphic with limited or no sexual size dimorphism (Nunes *et al.*, 2013), however sex differences in behaviour are also not uncommon in monomorphic seabirds (Lewis *et al.*, 2002; Pinet *et al.*, 2012).

Food resources are often scarce and patchily distributed in tropical marine environments (Abrams, 1985). Whilst provisioning for their chick, pelagic seabirds must therefore find an equilibrium between reaching productive areas, searching for prey, returning to the chick at regular intervals to feed and/or guard whilst the partner forages, and self-provisioning (Sommerfeld and Hennicke, 2010). Parental provisioning frequency and meal size can influence chick growth rate, along with attendance at the nest providing temperature regulation and protection from predators and rival territorial conspecifics (Schreiber, 1994).

Bimodal foraging strategies (alternating long and short foraging trips) such as those employed by tropicbirds (Sommerfeld and Hennicke, 2010) are known to influence body condition (Weimerskirch, 1998; Welcker *et al.*, 2012). This requires parent birds enduring extended fasting periods during incubation shifts, and balancing energy expenditure in provisioning for a chick with provisioning for themselves. Seabirds with long incubation periods typically lay a single egg clutch and fast whilst their partner is foraging at sea. The length of an incubation shift can substantially negatively affect adult body condition (Croxall, 1982), although the rate of loss of condition is influenced by individual differences in metabolic rates (Shoji *et al.*, 2015). Chick provisioning periods in pelagic seabirds are also typically extended. These life history traits render species such as

tropicbirds particularly vulnerable to unpredictable variations in food resources (Ballance and Pitman, 1999). There is a lack of knowledge of tropicbird chick growth rates, which have either been poorly documented and/or date from estimates obtained decades ago, when foraging conditions may have been very different (Stonehouse, 1962; M. P. Harris, 1969; Fleet, 1974; Phillips, 1987).

Chick growth and adult body condition can also vary among breeding seasons and different localities, due to inter-annual variation in oceanographic conditions caused by El Niño Southern Oscillation (ESNO) and the Pacific Decadal Oscillation (PDO) which affect upwelling, ocean productivity and food availability, in turn leading to changes in parental foraging effort and nest attendance behaviour of seabirds (Clark, W. Schreiber and Schreiber, 1990; Schreiber, 1994; Polis *et al.*, 1997; Blight *et al.*, 2010; Castillo-Guerrero, Guevara-Medina and Mellink, 2011; Champagnon *et al.*, 2018). In the South Atlantic, south-east trade winds create interannual fluctuations of the Angola Benguela upwelling system, leading to warm 'Benguela Niño' and cold 'Benguela Niña' events (Feistel, Hagen and Grant, 2003). Yet, in comparison to climate and oceanographic oscillations in the Pacific Ocean, where the effects have been extensively studied, little is known whether or how these oscillations might impact tropical south Atlantic ecosystems. Many seabird populations are located adjacent to continental shelves, where coastal upwelling systems can influence productivity, and thus local food availability can also influence adult body condition, breeding performance and foraging behaviour (Simeone *et al.*, 2002; Becker and Peery, 2007; Pereira *et al.*, 2020). In contrast, isolated oceanic populations that are out of reach of the coast or nearby land masses may be reliant on deep-sea topographical features, such as seamounts for enhanced prey availability.

In this study I aimed to test several hypotheses about the role of body condition in mediating the breeding behaviour of Red-billed Tropicbirds (*Phaethon aethereus*), largest and least numerous tropicbird species with a globally declining population (McGehee, 2000). Firstly, I tested for between-year differences in adult body condition, predicting that adults would exhibit poorer body condition in years with reduced food availability possibly mirroring variation in the environment among years. Secondly, I tested for changes in adult body condition between and within breeding stages, expecting that body condition would decline across the breeding season due to energetic constraints and that body condition would be negatively associated with the length of individual incubation shifts when the incubating bird is unable to forage. Thirdly, I tested the null hypothesis of equal parental incubation and provisioning effort between the two sexes, predicting that due to the limited sexual size dimorphism of Red-billed Tropicbirds (Nunes *et al.*, 2013) parental investment is likely to be similar between the sexes. Fourthly, I tested for differences in

parental body condition at nests with differing reproductive outcomes (success or failure), expecting that breeding failure would be associated with poor parental body conditions. Finally, I compared chick growth rates between two localities in the Atlantic Ocean: an oceanic (St Helena) and neritic (Cabo Verde) population, predicting that because marine resources are more patchily distributed in large pelagic oceanic regions than in areas with predictable upwelling systems with higher prey availability, that chick growth rates would be lower in chicks from St Helena than in chicks from Cabo Verde.

4.3. Methods

4.3.1. Study sites

This study was conducted in two regions of the Atlantic Ocean (Figure 4.1a); St Helena in the central south Atlantic (15° 57' S, 5° 42' W) and Cabo Verde in the central eastern Atlantic (16° 00' N, 24° 00' W). St Helena is located on the eastern edge of the South Atlantic subtropical gyre in the path of the south-east trade winds and the South Equatorial Current (Talley *et al.*, 2011). Cabo Verde, consists of 10 volcanic islands that lie between 600 and 850km west of Senegal, Africa (Figure 4.1a, c), located at the eastern boundary of the North Atlantic subtropical gyre at the southern limit of the Canary Current (Fernandes *et al.*, 2005). The waters around St Helena are characterised by a generally low chlorophyll *a* concentration with substantial variation in spatial distribution between years (maximum range 0.3--0.5mg/m³ (Thorpe *et al.*, 2020), whereas Cabo Verde is considered a more productive oceanic region with more enriched waters (chlorophyll *a* concentration range 0.06-4.1 mg/m³ (Vieira, 2019; Medrano, Militão, *et al.*, 2022; Silva, 2022)).

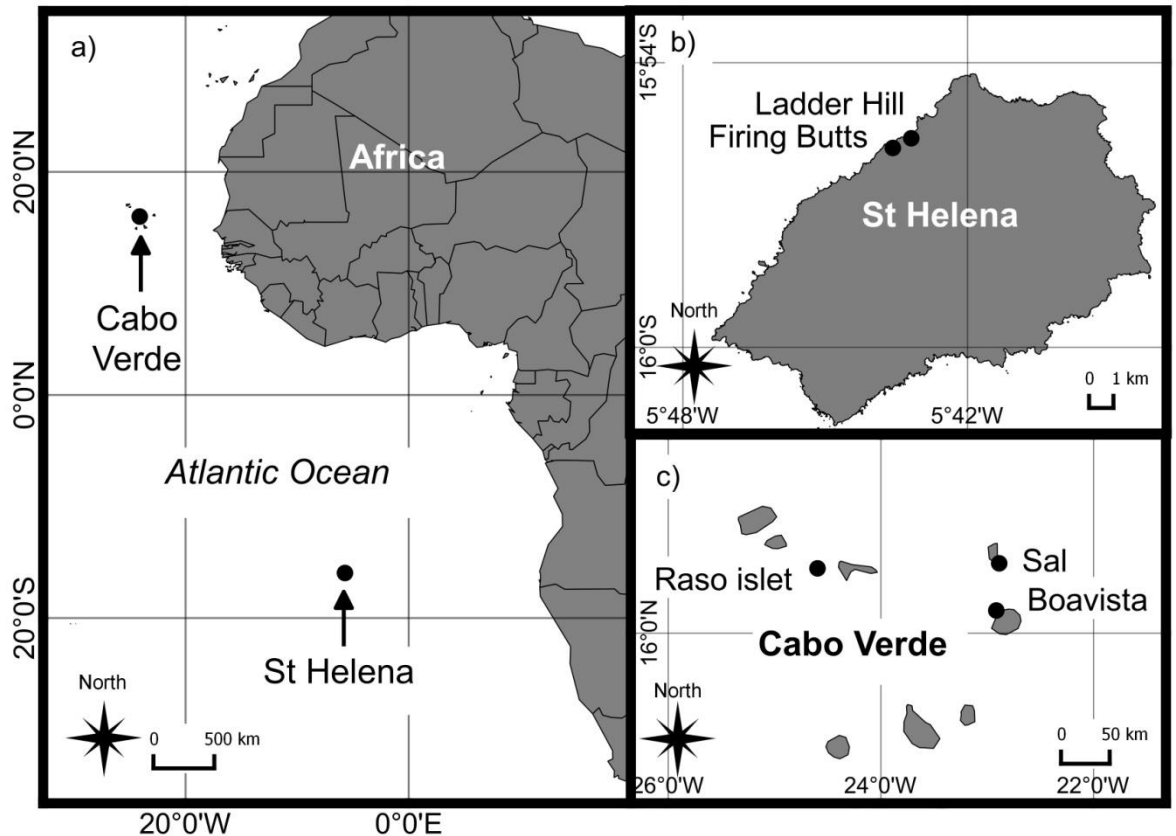


Figure 4.1. Location of the two study regions of Red-billed Tropicbirds in a) the tropical Atlantic Ocean, b) St Helena and c) Cabo Verde. Black circles indicate study sites.

4.3.2. Adult body condition

I obtained 1061 measures of adult body mass from 122 individuals as a reliable index of body condition (Labocha and Hayes, 2012). A minimum of 24 cavities per year were monitored between 21st August and 21st December, over a five year period (2013-2017) at St Helena, using a combination of direct observations and infra-red motion sensor cameras (see Chapter 2, Table 2.2 for details). Whenever possible, Bushnell Trophy Cameras were positioned near the entrance of cavities so that the arrival and departure of adults were continuously monitored. All adults in cavities were caught by hand and fitted with a standard metal ring (issued by the British Trust for Ornithology; BTO) on their right tarsus, weighed and measured followed Redfern and Clark (2001). To enable individual identification of breeding pairs without frequent capture or handling, any breeding adults were marked with a unique combination of colour marks on their head feathers (dyed with non-toxic waterproof markers; Sharpie) under licence by the BTO (licence S5526). Each nest in a cavity was given a unique nest identification number to identify individual nesting attempts. Here I define pre-breeding body condition as the mass of adults weighed within the seven day period prior to egg laying. Incubation body condition was defined as the mass of adults while sitting on an egg in a nest, chick rearing body condition as the mass

of adults which were attending a chick on a nest, and non-breeding body condition as the mass of adults which were not known to be actively breeding at the time of weighing.

Fieldwork was conducted at two monitoring plots on St Helena (Ladder Hill and Firing Butts, Figure 4.1b) and two islands (Sal and Boavista) and one islet (Raso) in Cabo Verde, each containing accessible Red-billed Tropicbird nesting cavities. Individual Red-billed Tropicbirds usually have an annual breeding cycle, but the species can be found breeding throughout the year at both study sites, with a seasonal peak in productivity; October to May at Cabo Verde (Diop *et al.*, 2019) and July to January at St Helena (Chapter 2). Tropicbirds have an extended incubation period (~43 days; Stonehouse (1962)) with incubation shifts lasting up to 16 days (Fleet, 1974) and chick rearing period that can last 12-13 weeks before fledging (Boeken, 2016). Red-billed Tropicbird populations were estimated to be up to 246 pairs at St Helena (Chapter 2) but as many as 1100 pairs at Cabo Verde (BirdLife International, 2023).

Where possible, for each adult during incubation, I estimated the following covariates along with its weight; 1) The number of elapsed days of the incubation period (Incubation period days) when the adult was weighed. The incubation period (assuming up to 43 days (M. P. Harris, 1969)) was defined as the number of days from laying an egg to hatching a chick, based on known laying and/or hatch dates. 2) The total length (in days) of the individuals incubation shift (Incubation shift length). This was recorded from an incubating adults first day on the nest to the last day before the relieving mate returned to the nest. 3) The proportion of the individual incubation shift completed at the date of weighing (Incubation shift proportion: day of incubation shift/Incubation shift length), as incubation shift length can vary during the incubation period. 4) Incubation outcome (hatching success; true/false). 5) The year the adult was monitored (2013-2017), and 6) the sex of the adult (male or female) which was determined following standard molecular sexing methods from feather samples collected during fieldwork (Fridolfsson and Ellegren, 1999) (see Appendix 1 for details). When weighing adults rearing chicks, we estimated the age of the chick (in days) based on the date the chick was first discovered hatched and/or known fledging dates, assuming a 93 day chick rearing period (M. P. Harris, 1969) and the growth stage of plumage (Stonehouse, 1962).

4.3.3. Breeding regime

Incubation shifts at St Helena were calculated using a combination of 1) camera trap images with date and time stamp showing an adult returning to the cavity to change over incubation duties with its partner subsequently leaving the cavity, and when such images of a changeover event were not available 2) the mid-point between two consecutive observations, where different adults were observed. Parental attendance during the chick

rearing period was quantified by calculating the proportion of observations where at least one parent was present on the nest with the chick. A chick was deemed fledged if it was at least circa 85 days old (Boeken, 2016) known to weigh at least 500g and absent from its cavity during subsequent observations, and/or camera images showed the chick leaving the cavity entrance at a near-fledged stage.

4.3.4. Chick biometrics

Standard biometric measurements (weight: mass to the nearest gram using a Pesola spring balance, wing cord: flattened wing from the carpal joint to the tip of the longest primary, tarsus: maximum tarsus length from the distal point of the inter-tarsal joint to the foot, head-plus-bill: bill tip to the posterior ridge formed by the parietal-supraoccipital junction, culmen length: exposed culmen and nostril to bill: length from the distal end of the nostril to the tip of the bill using a calliper to the nearest 1mm) were obtained following Redfern and Clark (2001) for all chicks at St Helena in the 2017 breeding season. Chick biometric data at Cabo Verde were pooled from the two island and one islet (Sal, Boavista and Raso respectively, Figure 4.1c) during the equivalent breeding season in 2017. A subset of biometrics (weight, wing, head and bill, culmen length) was selected from Cabo Verde chicks with known hatch dates within a <15 day accuracy for a regional comparison of chick growth with St Helena. Estimated chick age since hatching and biometrics were recorded every second day at St Helena and a maximum of five days at Cabo Verde until either the breeding attempt failed, or the chick fledged.

4.3.5. Statistical analysis

All statistical analyses were carried out in the statistical program R 3.5.1 (R Development Core Team, 2021) implemented in R-studio. All generalised linear mixed models (GLMMs) were implemented in the package *lme4* (Bates *et al.*, 2015), all likelihood ratio tests (LRTs) in the *lmttest* package (Zeileis and Hothorn, 2002) and all generalized additive mixed models (GAMMs) in either the *gamm4* package (Wood & Scheipl, 2020) or *mgcv* package (Wood, 2004), following Thomas *et al.*, (2017). Significant effects in final models were plotted using the R packages *ggplot2* (Wickham, 2016), *ggpubr* (Kassambara, 2020), *hrbrtheme* (Rudis, 2020). Estimated parameters for the growth curves were calculated in the R package *FlexParamCurve* (Oswald *et al.*, 2012).

4.3.5.1. Body condition

I tested for any effect of the monitoring period (Julian day) on adult body condition using a GAMM with a thin-plate regression spline, gamma error family and log link function. To control for repeated measures of individuals and locations (pseudo-replication), individual identity and cavity identity were both included as random effects.

I used GLMMs to test the hypothesis that body condition would vary by (1) sex, (2) breeding stage and (3) the interactive effect of sex and breeding stage. Body condition was treated as a normally distributed response variable using "log" link function and also included individual identity and cavity identity as random effects in the model. For each variable (sex, breeding stage or sex:breeding stage), I constructed two models: one containing the variable as a fixed effect, and a null model without the variable as an effect, then compared the two models using a LRT (Lewis, Butler and Gilbert, 2011). I concluded that the variable was a significant predictor of body condition if the model containing the variable of interest was significantly better than the null model (threshold $p < 0.05$). I also tested for differences in body condition between years using the same model structure described above but included breeding stage as a fixed factor in both models.

I used GLMMs to assess whether body condition during the incubation and chick rearing breeding phase differed between sexes, years, breeding outcome (hatched: true/false, fledged: true/false), or date within the breeding phase. For body condition during the incubation period I included additional variables: the length of incubation shift: excluded incubation shifts that extended past the average incubation period (43 days Harris (1969) in case incubation shift length was influenced by breeding outcome) and the proportion of incubation shift completed. For the chick rearing period I also included the age of the chick (in weeks, up to 10 weeks of age) as a factor. For each variable and breeding stage I constructed two models: one containing the variable as a fixed effect, and a null model. Given that the data comprised multiple body weights from the same individuals and nesting attempts, I included the random effects of individual identity (Ring ID) and nest identity (Nest ID) within each GLMM. A gamma distribution with a log link function was used to model the response variable (body mass). I compared the two models using a LRT as detailed above.

I then further explored which variables that were identified as significant from the LRTs (detailed above) best explained variation in body condition during incubation. To do this I constructed a global model with each variable included as an additive term and as a two-way interaction with each other variable. Model selection was performed by sequentially removing the least significant term until the model with the lowest Akaike's Information Criterion (AIC) value was identified (Burnham and Anderson, 2002).

4.3.5.2. Incubation shifts

Descriptive statistics were generated for incubation shift frequency using a subset of data from pairs containing individuals of known sex, that were monitored from laying to hatching, and where the shift sequence could be identified. I used GAMMs to explore whether variation in the time spent incubating an egg could be explained by any

differences between sexes, years, hatching outcome or incubation periods. Given that our data were comprised of multiple incubation shifts from the same individuals and nesting attempts, I included the random effects of individual identity and nest identity. A gamma distribution with a log link function was used to model the response variable (Incubation shift length). Smoothed terms were fitted to the day of incubation period (Incubation period days) with a penalised regression spline (Wood and Augustin, 2002; Thomas *et al.*, 2017). The full model included sex, hatching outcome and year as additive terms, as well as an interaction between sex and day of incubation period, hypothesising that incubation shift length may differ between successful and unsuccessful nests, years and sexes. The interactive effect of sex and day of incubation period was included, as tropicbirds are known to alternate incubation duties between sexes (Boeken, 2016). Model selection was based on a stepwise deletion process, by removing the least significant term at each step, evaluated by an ANOVA test and resulting change in AIC value until the model with the lowest AIC value was identified.

4.3.5.3. Mass loss during incubation

The rate of mass loss is a reliable index of energy costs incurred by fasting birds during incubation (Croxall, 1982). The rate of mass loss during incubation was examined using the proportion of mass loss per day, calculated from a subset of masses during incubation from individuals that had more than one mass measurement during the same incubation shift. The difference between the two mass measures was divided by the number of days between measures, divided by the initial mass x100 to give the proportional mass loss per day, for each individual. To investigate if the rate of mass loss during an incubation shift varied between years, sexes and between incubation outcome (hatching success: true/false) I then constructed two competing GLMMs with proportional mass loss per day as the response variable (one containing the variable as a fixed effect, and a null model without the variable as an effect, then comparing the two models using a LRT) to identify any effect of each variable (year, sex, incubation outcome) independently. I then explored if the variables identified as significant during incubation (proportion of incubations shift completed, incubation shift length, day of incubation period, defined above) also influenced proportional mass loss per day. For this I constructed a global model from which the least significant terms were removed stepwise until the model with the lowest AIC value was identified.

4.3.5.4. Parental attendance during chick rearing

Descriptive statistics on the proportion of visits where parents were present with chicks on the nest were generated to identify changes in parental attendance through the chick rearing period, firstly by the age of the chick in weeks and secondly by the age groups

defined by Stonehouse (1962) to allow for a regional comparison with Ascension Island. Binomial tests were used to examine (1) any differences in overall attendance between St Helena and Ascension Island, and (2) differences in parental attendance between nests that failed and nests that successfully fledged a chick at St Helena, hypothesising that more attentive parents would have better breeding success.

4.3.5.5. Chick growth

The growth rate and variation in chick body mass between the two regions was explored by fitting logistic growth curves (Richards, 1959) using the equation:

$$y = A / (1 + m \times e^{-k \times (age - i)})^{1/m}$$

where y is the response variable (weight, wing, tarsus, head and bill, culmen and nostril to bill length), A represents the asymptote, k the rate at which the slope of the curve changes with age, i the inflection point corresponding to the age at which the fastest growth is achieved, and m the shape parameter of the logistic curve (Richards, 1959).

To compare growth rates between geographical regions, I calculated the proportion of growth per day for each chick, firstly by calculating the difference in mass between two consecutive measures, then dividing the difference by the number of days between measures, and by the initial mass. This gave the proportion of mass lost per day. A Gaussian GAMM with "identity" link function was then used to test for effects of region on the proportion of growth by chick age. Nest identity was treated as a random effect to account for repeated measures from individual chicks, and region as a fixed factor.

4.4. Results

4.4.1. Influences on adult body condition

There was no significant linear association of adult body condition with Julian day ($P = 0.251$, $R^2 = -0.00169$, $F = 0.411$, $n = 1061$), but pre-breeding adults ($n = 31$) were on average 91g heavier than adults rearing chicks and 70g heavier than non-breeding adults (LRT $X_3^2 = 76.888$, $P < 0.001$; Figure 4.2). After accounting for differences between breeding stages, body condition also differed significantly between years (LRT $X_4^2 = 11.261$, $P = 0.024$); adults during 2015 ($n = 241$) were lighter (mean 710 ± 68 g) than in the other four years monitored (Figure 4.3). Although males were on average slightly heavier than females 728 ± 67 g, $n = 554$ and 714 ± 73 g, $n = 507$ respectively) there was no significant difference in body condition between sexes (LRT $X_1^2 = 0.007$, $P = 0.933$), or between the sexes during different breeding stages (interaction term; LRT $X_3^2 = 3.2187$, $P = 0.359$).

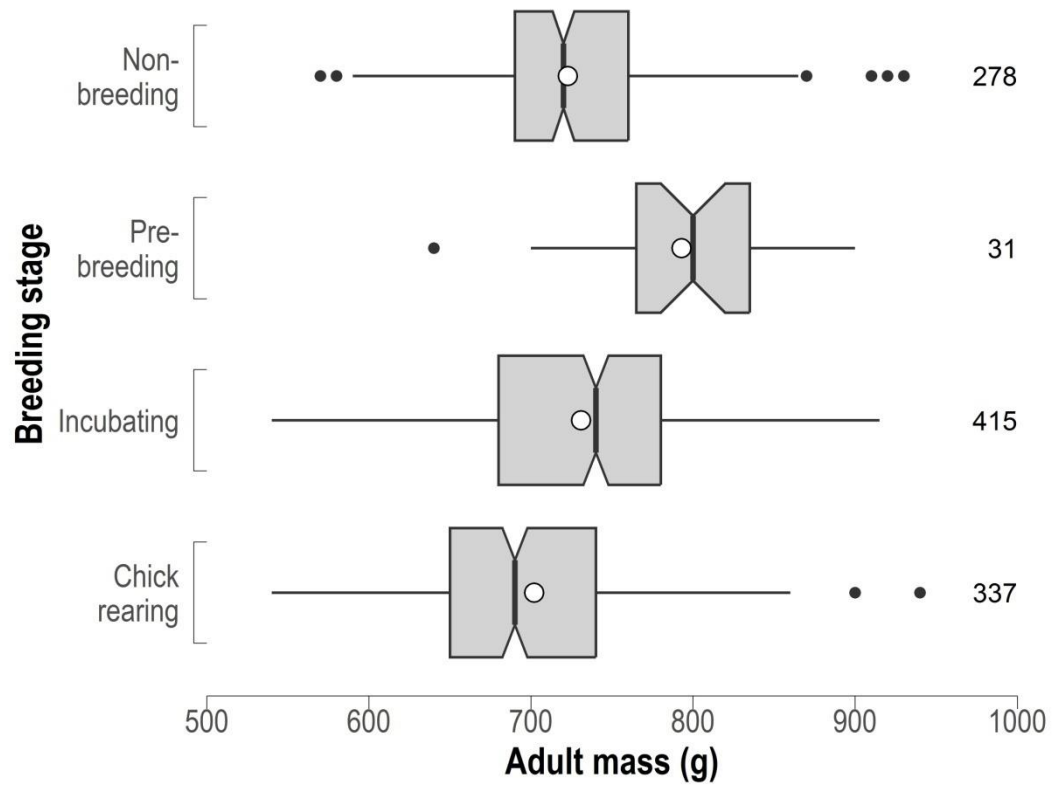


Figure 4.2. Body condition (mass in grams) of adult Red-billed Tropicbirds at different breeding stages at St Helena, South Atlantic. Boxplots show median values (thick vertical bar) per breeding stage, including 95% confidence intervals of the median (notches), 25th and 75th percentiles (grey boxes), ranges within 1.5 times the width of the box (horizontal whisker lines), outliers (black points) and means (white points). Sample sizes are shown on the right of the plot.

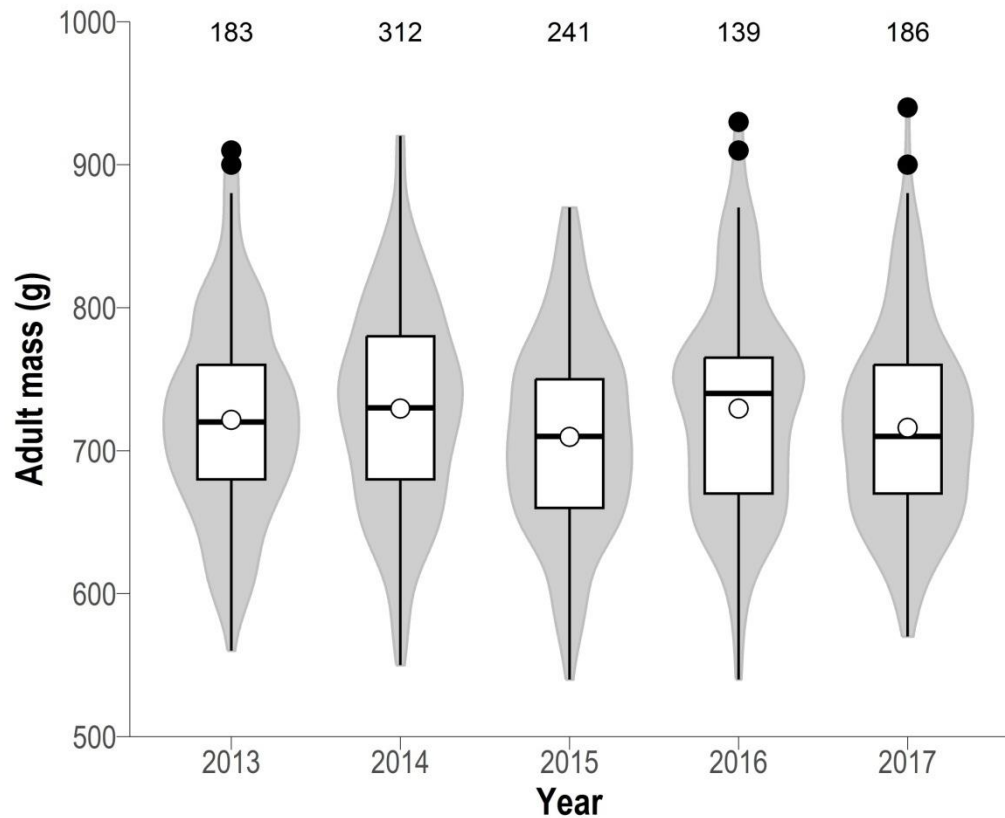


Figure 4.3. Temporal variation in body mass of adult Red-billed Tropicbirds between 2013-2017 at St Helena Island, South Atlantic. Sample sizes are indicated at the top. Violin plots show the adult mass density distribution during each year. Black-contoured boxplots show median (line), 25th and 75th percentiles (boxes), ranges within 1.5 times the height of the box (whiskers), outliers (black points) and means (white points). Sample sizes are shown at the top of the plot.

4.4.2. Changes in body condition during the incubation period

Body condition during incubation was significantly negatively associated with the length of the incubation shift being undertaken (incubation shift length; LRT $\chi^2 = 4.481$, $P = 0.034$), the proportion of the incubation shift they had completed (incubation shift proportion; LRT $\chi^2 = 280.16$, $P < 0.001$) and how far they were into their incubation period (incubation period days; LRT $\chi^2 = 8.3425$, $P = 0.004$, all $n = 382$). Adults that successfully hatched an egg were only marginally heavier (mean, $733 \pm 69.8\text{g}$, $n = 268$) than those that failed (mean $724 \pm 80.9\text{g}$, $n = 110$; LRT $\chi^2 = 0.5745$, $P = 0.448$, $n = 378$). There was also no evidence that body condition during the incubation period differed between the sexes (males; mean $736 \pm 74.1\text{g}$, $n = 178$, females $727 \pm 71.4\text{g}$, $n = 174$, LRT $\chi^2 = 0.058$, $P = 0.810$, $n = 352$) or between years they were monitored (LRT $\chi^2 = 3.162$, $P = 0.531$, $n = 387$).

The model that best described variation in body condition over the incubation period included the proportion of the incubation shift completed (Incubation shift proportion), and the length of the incubation shift undertaken (Incubation shift length), both as individual main effects, and as an interactive effect ($R^{2m} = 0.467$, $R^{2c} = 0.710$, $n = 387$, Table 4.1). Incubation shift proportion significantly negatively affected body condition; adults that had completed more than half of the shift were on average 99g lighter (mean $664 \pm 56g$, $n = 117$) than those still completing the first half of the shift (mean; $763 \pm 57g$, $n = 248$). Likewise, incubation shift length significantly negatively affected body condition; tropicbird undertaking long incubation shifts (7-13 days in length) were on average 16g lighter (mean; $726 \pm 77g$, $n = 248$) than those undertaking short incubation shifts (1-6 days in length, mean; $741 \pm 63g$, $n = 139$). Tropicbirds entering long incubations shifts had higher body mass at the start of their incubation shift than tropicbirds entering short incubations shifts (Figure 4.4a). Tropicbirds were much lighter by the end of long incubations shifts than at the end of short incubation shifts (Table 4.1, Figure 4.4b).

Table 4.1. Results of generalized linear mixed models (GLMMs) assessing which variables were associated with Red-billed Tropicbird mass during incubation at St Helena, using individual identification (Ring ID) and nest identification (Nest ID) as random effects (top section), and parameter estimates of variables in the most parsimonious model (bottom section).

Competing models					
Model	Random effects	k	AICc	Delta AIC	AICcWt
(4) - Incubation period days: Incubation shift length	Ring ID + Nest ID	7	3999.46	0.00	0.40
(3) - Incubation days	Ring ID + Nest ID	8	3999.65	0.19	0.36
(2) - Incubation shift proportion: Incubation period days	Ring ID + Nest ID	9	4001.10	1.64	0.18
(1) Global ^a	Ring ID + Nest ID	10	4003.18	3.72	0.06
Significance of variables included in model (4)					
Variable	estimate	std error	t	P value	
Incubation shift proportion	-0.063	0.003	-21.998	< 0.001	
Incubation shift length	-0.008	0.004	-2.223	0.026	
Incubation shift proportion: Incubation shift length	-0.020	0.003	-7.155	< 0.001	

^a The global model contained all variables previously identified as significant predictors of body condition during incubation by LRTs; (Incubation shift length, incubation shift proportion, and day of the incubation period (Incubation period days) included as additive and two-way interaction effects. Other models denote the term that is removed from the global model, and the resulting change in AICc. Model selection was based on AICc. k denotes the number of estimated parameters for each model. Akaike weights are represented as AICcWt. Significant P values are in bold.

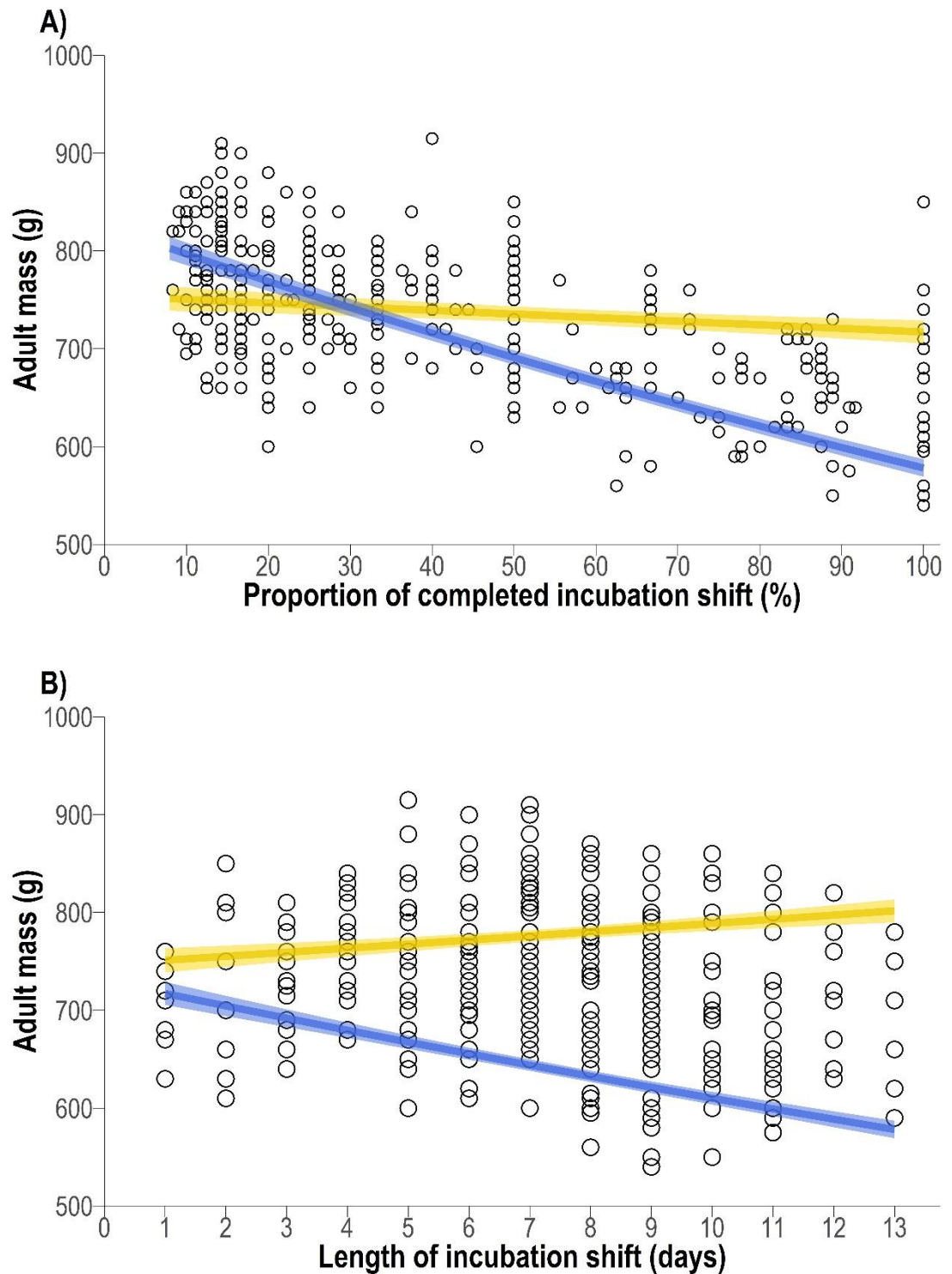


Figure 4.4. Variation in body mass of adult Red-billed Tropicbirds during incubation, showing that body mass was influenced by both the proportion of the incubation shift that has been completed, the overall length of the incubation shift, and the interaction between these two variables. Open circles represent raw data, solid lines represent model predictions, and shaded areas around the fitted lines represent $\pm$ SE. **A)** Body mass

versus proportion of completed incubations shift. The yellow line represents model predictions for the shortest incubation shift (shift duration = 1 day), and the blue line represents the longest incubations shift (13 days). **B)** Body mass versus incubation shift length (1-13 days). The yellow line represents model predictions for early in the incubation (8.3% of the shift completed), and the blue line represents model predictions for the end of the incubation shift (100% of the incubations shift completed).

4.4.3. Incubation shifts and mass loss

Red-billed Tropicbird parents alternated incubating the egg in shifts, completing an average of 7.61 ± 1.20 shifts (range: 6-11 shifts, $n = 23$ nests) through the incubation period, with each shift lasting on average 6.04 ± 2.76 days (range < 1 - 12 days, $n = 314$; Table 4.2). The model that best described variation in incubation shift length included an interaction between the day of the incubation period and sex, as well as incubation period, sex and year as main effects (Table 4.3). The incubation shift length was strongly influenced by parent sex, and by the day of the incubation period (Table 4.3 (bottom section), Figure 4.5). The first shift completed by the female after she had laid the egg was usually short (1.40 ± 1.44 days, Table 4.2), and shift length of both sexes decreased as hatching approached (Table 4.3, Figure 4.5). Males were more likely to complete longer incubation shifts than females ($\beta = 0.269 \pm 0.065$ SE, $P < 0.001$, $t^1 = 4.136$), lasting on average one day longer (male mean shift length 6.44 ± 2.75 days, range 0.07-11.8, $n = 148$; females: 5.51 ± 2.94 days, range 0.01-11.9, $n = 145$). There was also considerable variation in shift length between years ($P = 0.007$, $F_4 = 3.616$), incubation shifts during 2015 were on average the longest, lasting 7.00 ± 2.10 days, (range 0.94-11.8, $n = 54$), compared to the shortest shift lengths in 2016, lasting on average 5.15 ± 3.58 days, (range 0.01-11.8, $n = 46$). Nesting attempts that successfully hatched an egg completed only marginally longer incubation shifts than those that did not ($P = 0.185$, $F_1 = 1.765$, hatched: 6.07 ± 2.52 days, range 0.10-11.8, $n = 229$, failed 5.48 ± 3.67 days, range 0.01-11.9, $n = 60$).

Table 4.2. Mean ($\pm$ s.d.) duration of incubation shifts in Red-billed Tropicbirds from 37 monitored nests at St Helena 2013-2017.

Shift	Sex ¹	Duration (days)	Range	n
First	F	1.40 $\pm$ 1.44	0.04-6.99	27
Second	M	6.75 $\pm$ 1.96	2.07-11.0	33
Third	F	6.94 $\pm$ 2.10	2.00-11.8	33
Fourth	M	7.60 $\pm$ 2.28	3.01-11.8	33
Fifth	F	7.26 $\pm$ 2.33	0.95-11.9	31
Sixth	M	6.73 $\pm$ 2.24	2.57-11.6	31
Seventh	F	5.93 $\pm$ 1.64	2.85-8.92	17
Eighth	M	4.62 $\pm$ 2.72	1.61-10.6	11
Ninth	F	3.34 $\pm$ 1.98	1.13-4.97	3
Tenth	M	2.03		1
Eleventh	F	2		1

¹ F = female, M = male.**Table 4.3.** Generalized additive mixed models (GAMMs) assessing which variables were associated with incubation shift length of Red-billed Tropicbirds at St Helena, using individual identification (Ring ID) and nest identification (Nest ID) as random effects (top section), and parameter estimates of variables in the most parsimonious model (bottom section).**Competing models**

Model	Random effects	AICc	BIC	LogLik
(3) - Hatching success	Ring ID + Nest ID	1450.3	1497.9	-712.1
(2) - Incubation period days	Ring ID + Nest ID	1451.2	1502.5	-711.6
(1) Global ^a	Ring ID + Nest ID	1453.2	1508.2	-711.6

Significance of smoothed terms in model 3

Variable	edf	F	P value
Incubation period days: Female	4.355	63.10	< 0.001
Incubation period days: Male	1.994	11.55	< 0.001

^a The global model contained sex, hatching success and year as additive terms, the day of incubation period (Incubation period days) a smoothed additive term as well as an interaction between sex. Other models denote the term that is removed from the global model and the change in AICc this produced. Model selection is based on AICc. Significant *P* values are in bold.

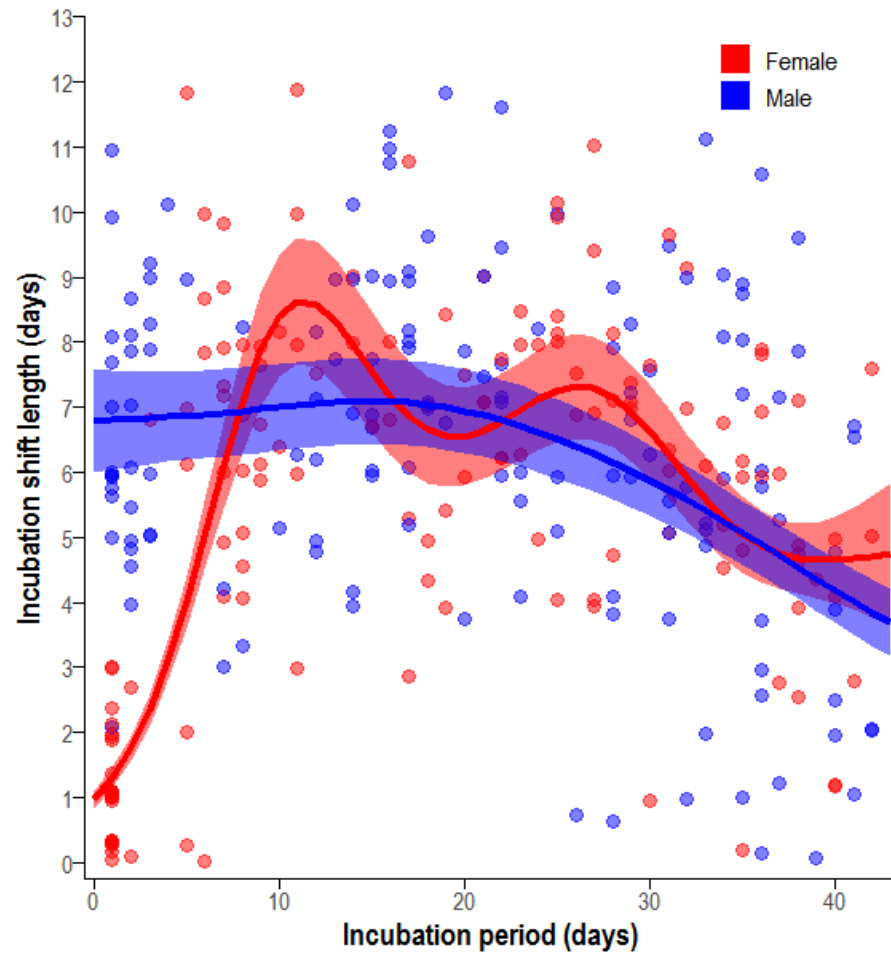


Figure 4.5. Variation in the incubation shift length (consecutive time spent incubating an egg) throughout the incubation period, in male (blue) and female (red) Red-billed Tropicbirds at St Helena. Predicted values (line $\pm$ 1 SD) are based on the final GAMM model (Table 4.3, bottom section), using 2013 as the reference year.

The proportion of an incubation shift completed by adult Red-billed Tropicbirds was negatively related to the proportion of mass lost per day (LRT $\chi^2 = 9.689$, $P = 0.002$, $n = 88$), with an average of 4.1% (34g), (range 2.7-5.9%, 20 - 50g, $n = 6$) of body mass loss per day within the first half of a shift compared to 2.7% (21g) (range 0.4-5.6%, 3-47g, $n = 79$) of body mass lost per day in the last half of an incubation shift. There was no evidence that the proportion of mass loss per day differed between sexes, years, hatching outcome, incubation shift length or day of the incubation period (Sexes; ; LRT $\chi^2 = 0.1892$, $P = 0.664$, male; $n = 40$, female; $n = 48$, years; LRT $\chi^2 = 1.330$, $P = 0.856$, $n = 88$, incubation outcome; LRT $\chi^2 = 0.080$, $P = 0.777$, hatched; $n = 50$, failed; $n = 38$, incubation shift length LRT $\chi^2 = 0.603$, $P = 0.437$, $n = 88$, day of incubation period LRT $\chi^2 = 0.199$, $P = 0.655$, $n = 81$).

The model that best described the proportion of mass lost per day included the proportion of the shift completed and incubation shift length as additive effects ($R^{2c} = 0.202$, $R^{2m} = 0.190$, $n = 81$, Table 4.4. (top section), Figure 4.6). Adults at the start of a shift lost a higher proportion of mass per day than those at the end of their incubation shift. There was also a marginal negative relationship between mass loss and the length of the shift being undertaken; the longer the shift the lower the proportion of mass loss per day (Table 4.4., bottom section).

Table 4.4. Generalized linear mixed models (GLMMs) assessing which variables were associated with Red-billed Tropicbird proportion of mass loss per day during an incubation shift, using individual identification (Ring ID) and nest identification (Nest ID) as random effects (top section) and parameter estimates of variables in the most parsimonious model (bottom section).

Competing models					
Model	Random effects	k	AICc	Delta AIC	AICcWt
(4) - Incubation period days	Ring ID + Nest ID	6	259.28	0.00	0.57
(3) - Incubation shift proportion: Incubation period days	Ring ID + Nest ID	7	260.80	1.52	0.27
(3) - Incubation shift proportion: Incubation shift length	Ring ID + Nest ID	8	262.48	3.20	0.12
(2) - Incubation shift length: Incubation period days	Ring ID + Nest ID	9	264.87	5.59	0.03
(1) Global ^a	Ring ID + Nest ID	10	267.47	8.18	0.01
Significance of variables in model 4					
Variable	estimate	std error	t	P value	
Incubation shift proportion	-0.160	0.047	-3.439	< 0.001	
Incubation shift length	-0.093	0.050	-1.840	0.066	

^a The global model contained all variables previously identified as significant predictors of body condition during incubation by likelihood ratio tests; (Incubation shift length, proportion of incubation shift completed (Incubation shift proportion), and day of incubation period (Incubation period days)) included as additive and two-way interactive effects. Other models denote the term that is removed from the global model and the change in AICc this produced. Model selection is based on AICc. k denotes the number of estimated parameters for each model. Akaike weights are represented as AICcWt. Significant P values are in bold.

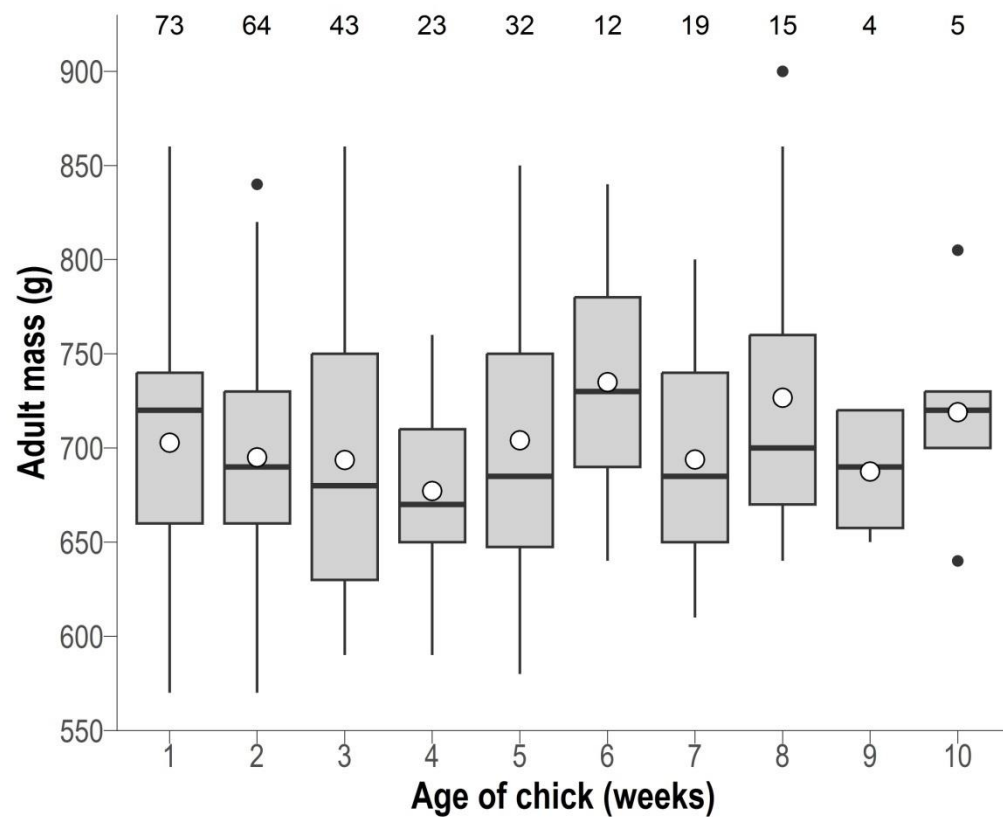


Figure 4.6. Relationship between adult body condition and chick age in weeks. Black-contoured boxplots show median (line), 25th and 75th percentiles (boxes), ranges within 1.5 times the height of the box (whiskers), outliers (black points) and means (white points). Sample sizes are shown at the top of the plot.

4.4.4. Parent attendance and body condition during chick rearing

Red-billed Tropicbird parents were found on the nest with the chick throughout its development until fledging, but parental attendance decreased substantially with chick age. Attendance was highest in the first two weeks of the chick's life, when parents were brooding and guarding the chick almost continuously, after which attendance reduced. Attendance during the fourth week of chick life showed the largest decrease, by almost 34% (Appendix 2, Table A2.1). Overall, adult Red-billed Tropicbirds at St Helena were present with the chick on a significantly higher proportion of visits than those observed by Stonehouse (1962) on Ascension Island ($P < 0.001$, $X_1^2 = 67.793$, St Helena; 54.9%, Ascension; 35.7%; Figure 4.7), although the temporal pattern of attendance through the age groups were similar on both islands. On St Helena, there was also no relationship between the proportion of visits where at least one parent was present and the proportion of nests that successfully fledged a chick ($P = 0.273$, $X_1^2 = 1.203$, fledged; 70.1%, failed; 73.6%).

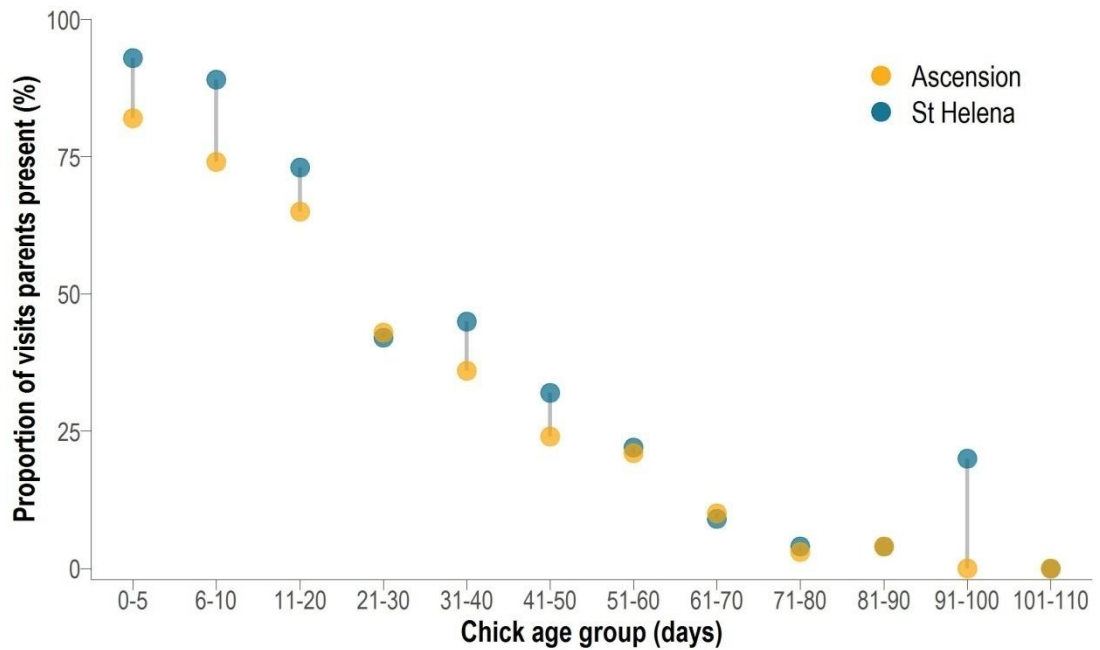


Figure 4.7. Relationship between the proportion of visits on which at least one parent was present, and chick age from two localities; St Helena 2013-2017 (blue) and Ascension 1957-1959 (yellow, from Stonehouse (1962)).

After accounting for repeated measures of individuals and nests, there was no significant difference in body condition between days during of the chick rearing phase (LRT; $X_1^2 = 0.023$, $P = 0.880$, $n = 290$), however body condition did vary significantly between weeks, notably adults rearing chicks at four weeks of age were likely to be lighter ($\beta = -0.057 \pm 0.019$, $t = -2.953$, $P = 0.003$), averaging 26g less (mean 677 ± 42 g, $n = 23$) than those rearing chicks in the first week of life (mean 703 ± 59 g, $n = 73$, Figure 4.6). There was no significant difference in body condition between the sexes (LRT; $X_1^2 = 0.157$, $P = 0.692$, male; $n = 140$, females; $n = 150$), between years (LRT; $X_4^2 = 1.606$, $P = 0.808$, $n = 290$) or between adults that successfully fledged a chick and those that did not (LRT; $X_1^2 = 0.911$, $P = 0.240$, fledged; $n = 178$, failed; $n = 112$).

4.4.5. Chick Growth

On St Helena twelve chicks were monitored from two up to 108 days after hatching, including eight chicks until fledging. At Cabo Verde, 22 chicks were monitored from a minimum of 7 days up to a maximum of 93 days after hatching, including seven chicks that were monitored until fledging. Growth curves were very similar across the two locations (Figure 4.8). Chicks from St Helena were heavier; the estimated asymptote of body mass was 760 g at St Helena and 695 g at Cabo Verde (Table 4.5). Body mass also showed larger fluctuations on St Helena, with chicks increasing up to 25% of their body mass per day, compared with only 5% at Cabo Verde. The maximum daily increase in

body mass at both locations was recorded when the chicks were between 20-30 days old; during this period some chicks increased their mass by up to 47% (336 g) per day at St Helena, and 17% per day (increase of up to 270 g per day) at Cabo Verde. Mean daily chick growth rates across the chick rearing period at St Helena were 3.6% of body mass and 2.1% of body mass at Cabo Verde (increase of 6.6 g/day and 7.4 g/day, respectively, assuming linear growth; for logistic growth curve parameters see Table 5, Figure 4.8). St Helena chicks gained significantly higher proportions of body mass per day than chicks from Cabo Verde (estimate 0.02%, $t = 2.454$, $P = 0.032$, Figure 4.9). A maximum body mass of 1,059 g was reached after 74 days at St Helena and 840 g after 63 days at Cabo Verde.

Table 4.5. Parameter estimates for logistic growth curves of Red-billed Tropicbird chicks in 2017 measured between age 2 and 108 days on St Helena ($n = 12$) and between 11 and 93 days of age ($n = 22$) for Cabo Verde.

St Helena						Cabo Verde			
Variable	Parameter	Estimate	SE	t	p	Estimate	SE	t	p
Weight	Asymptote	760.1	11.1	68.3	<0.001	698.1	13.6	51.3	<0.001
	m	1.1	0.5	2.1	0.039	9.3	7.5	1.2	0.215
	k	0.1	0.0	5.3	<0.001	0.2	0.1	1.5	0.136
	Inflection	25.9	2.4	11.0	<0.001	35.5	6.3	5.7	<0.001
Wing	Asymptote	314.2	8.1	38.7	<0.001	294.7	18.5	15.9	<0.001
	m	0.9	0.2	3.9	<0.001	1.6	1.0	1.7	0.095
	k	0.1	0.0	8.5	<0.001	0.1	0.0	2.9	0.004
	Inflection	49.6	1.2	40.0	<0.001	46.5	3.5	13.4	<0.001
Culmen	Asymptote	58.2	0.8	74.1	<0.001	53.7	1.5	36.1	<0.001
	m	-0.6	0.2	-3.0	0.003	2.9	2.6	1.1	0.266
	k	0.0	0.0	10.4	<0.001	0.1	0.0	2.5	0.013
	Inflection	1.8	3.3	0.6	0.575	19.1	10.5	1.8	0.071
Head and bill	Asymptote	118.2	0.9	134.9	<0.001	113.3	1.8	61.4	<0.001
	m	0.2	0.4	0.5	0.631	3.4	3.6	1.0	0.340
	k	0.1	0.0	10.4	<0.001	0.1	0.0	2.6	0.010
	Inflection	3.8	3.0	1.3	0.198	9.5	12.2	0.8	0.438
Tarsus	Asymptote	34.2	0.2	222.4	<0.001				
	m	1.8	0.9	2.1	0.040				
	k	0.1	0.0	7.1	<0.001				
	Inflection	6.8	2.6	2.6	0.009				
Nostril to bill	Asymptote	52.3	1.0	53.5	<0.001				
	m	-0.5	0.2	-2.3	0.021				
	k	0.0	0.0	8.4	<0.001				
	Inflection	3.9	4.0	1.0	0.329				

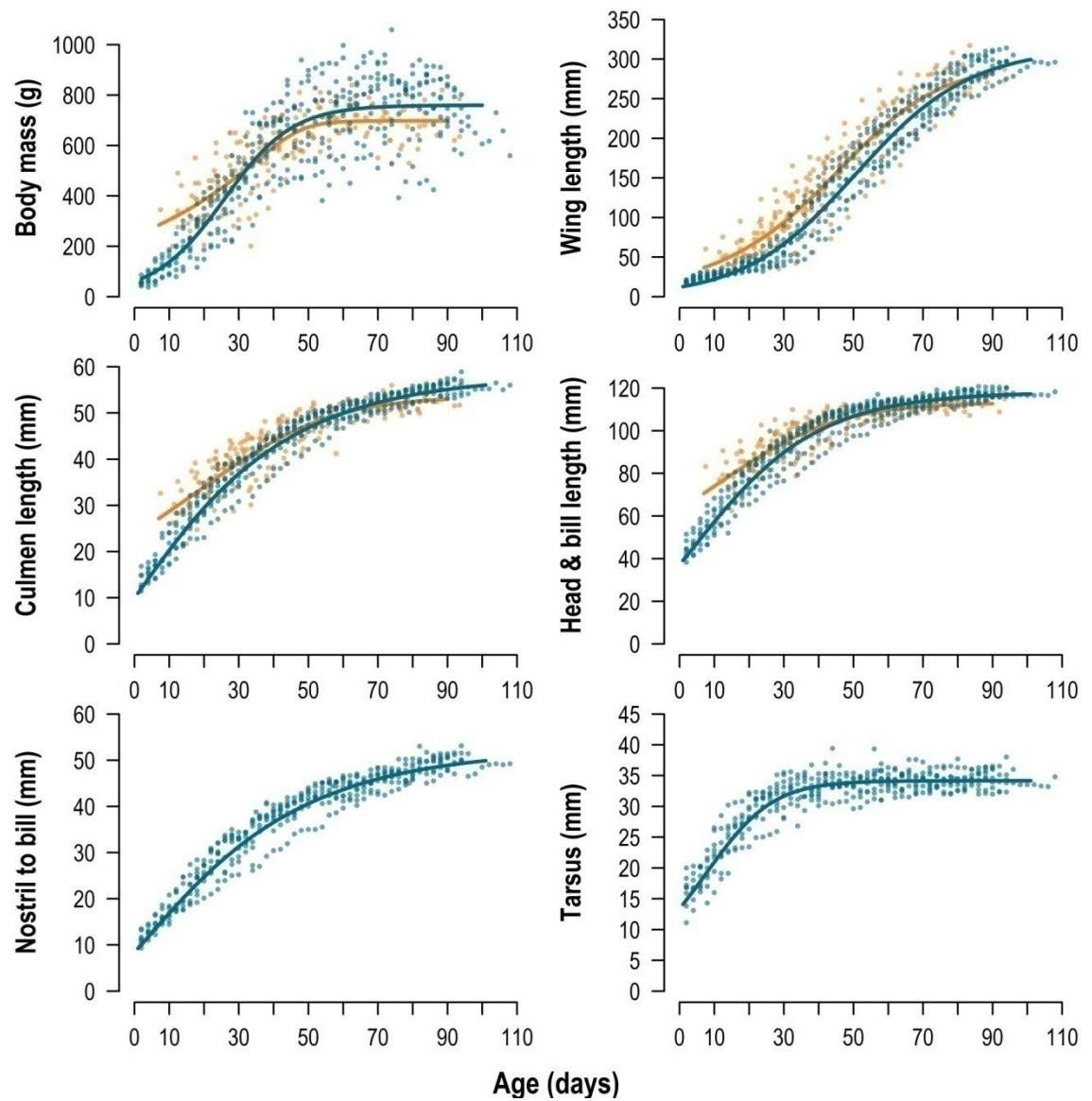


Figure 4.8. Growth rates of Red-billed Tropicbird chicks during the 2017 breeding season from two geographical regions; St Helena, $n = 12$ chicks: blue lines/circles and Cabo Verde, $n = 22$ chicks, orange lines circles. Lines are based on logistic growth curves (see Table 4.5 for parameter estimates). Nostril to bill and tarsus were not measured on Cabo Verde chicks. Body mass at both locations took approximately 60 days to reach as asymptote and wing length started to increase strongly after about 20 days when primary feathers started to grow. Structural variables relating to skeletal growth such as culmen length, head and bill length and nostril to bill at St Helena appeared to take about 60-80 days to reach an asymptote, whereas tarsus took approximately 40 days to reach asymptote on St Helena.

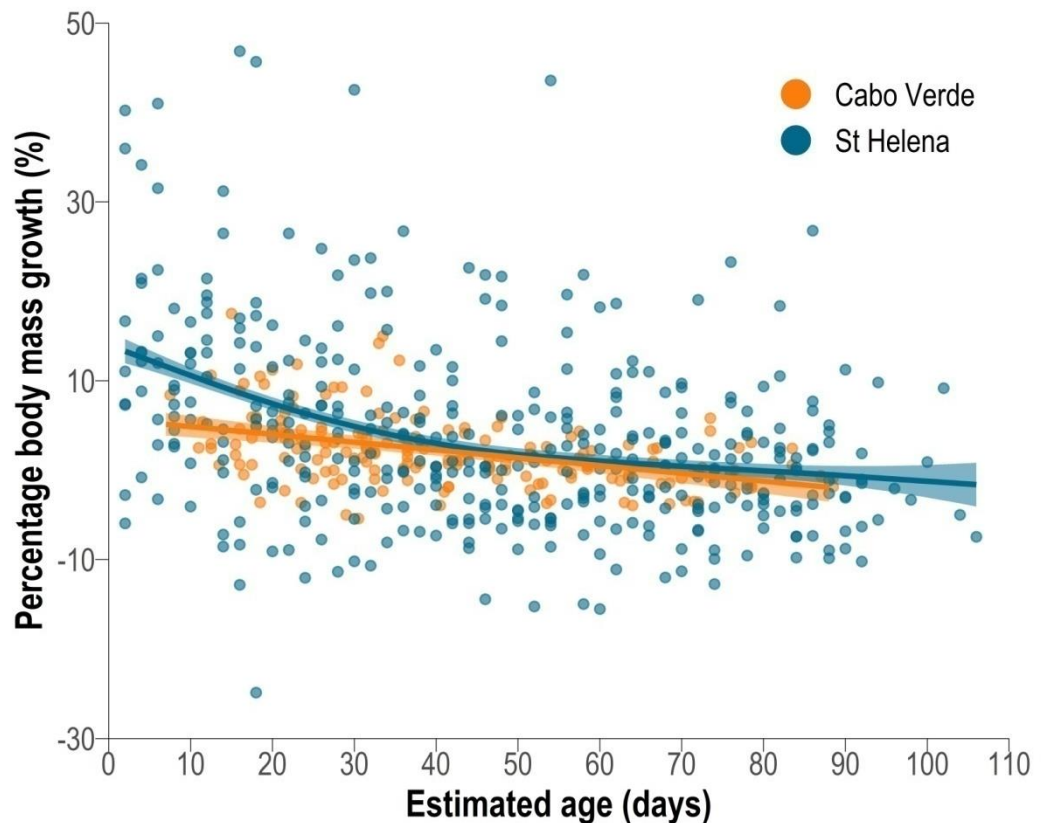


Figure 4.9. Comparison of daily proportion of body mass fluctuations with age in Red-billed Tropicbird chicks from two geographical regions (St Helena; blue lines/circles, Cabo Verde; orange lines/circles) during the 2017 breeding season. Lines are predictions from a GAMM ± 1 SE.

Maximum body mass of chicks from both locations was considerably greater than that of adults; at St Helena 147% of mean adult weight (721g, A. Beard, pers. obs.), and at Cabo Verde 133% of mean adult weight (631g, S. Saldanha, pers. comm.). Of the chicks that were monitored until fledging, body mass declined with increasing age; St Helena chicks lost on average 17g in the 10 days prior to fledging, and Cabo Verde chicks lost on average 25g over the same period (average decrease of 0.008%, $n = 8$ and 0.006%, $n = 7$ of body mass per day respectively). Although the final mass measured prior to fledging at St Helena (mean: 681g) was on average 5% lower than mean adult body mass at St Helena (mean: 721g), this apparent difference was not significant ($t = -1.81$, d.f. = 7.12, $P = 0.113$). At Cabo Verde, chicks were 2.7% heavier at fledging (mean: 648g) than the average adult. Chicks of fledging age from St Helena were also structurally smaller than an average adult; wing 6%, head and bill 2%, feathers to bill and nostril to bill were 8% smaller than the average adult reported by (Nunes *et al.*, 2013) from the Abrolhos archipelago off the coast of Brazil, but bigger than chicks at fledging from Cabo Verde; wing 6%, head and bill 4%, feathers to bill 8% bigger.

4.6. Discussion

This study is the first to provide a comprehensive examination of body condition influences on the breeding regime of a long-lived pelagic species providing bi-parental care. We found clear differences in adult body condition between years and life stages. The flexible sex-specific incubation routines: males undertook longer and more frequent incubation shifts than females were unexpected given that the species is considered monomorphic (Nunes *et al.*, 2013). We identified key aspects of the species breeding ecology such as incubation regime and chick growth, filling important knowledge gaps essential for the effective conservation and management of this globally threatened species.

4.6.1. Between-year variation in adult body condition at St Helena

Adult Red-billed Tropicbirds showed considerable year-to-year variation in body condition in my 2013-2017 study, with birds being significantly lighter during 2015 when adults also conducted significantly longer incubation shifts. This co-variation in adult body condition and incubation shift length suggests substantial inter-annual fluctuations in prey availability, with incubating adults in 2015 having to wait for longer periods for their partner to return from foraging at sea. Our study was conducted in part, during the austral winter (July-September) which is considered the peak in the Angola Benguela upwelling cycle (Hagen, Agenbag and Feistel, 2005). St Helena is directly in the path of the south-east trade winds which drives the South Equatorial Current bringing relatively enriched waters from the Angola Benguela upwelling current system towards the island. However whilst there were no extreme coastal warm or cold anomalous events during the study period that would be classified as a Benguela Niño or Niña (Lübbecke *et al.*, 2019; Imbol Koungue *et al.*, 2021), a moderate cold coastal event along the Angolan-Namibian coastlines did occur during 2015 (Imbol Koungue *et al.*, 2019). It is possible that the inter-annual fluctuations observed by this study, particularly during 2015 may be a consequence of variation in oceanographic conditions known to occur in the south-east Atlantic Ocean resulting from variability in the Benguela current upwelling system.

Environmental pressures and availability of resources may vary at different times of year, this may in turn also effect body condition and breeding regime. For example Red-tailed Tropicbirds (*Phaethon rubricauda*) on Round Island, Mauritius, which like Red-billed Tropicbirds at St Helena, breed year-round but with a degree of seasonality, were shown to have different flight efforts and costs in summer and winter (Shepard, 2021). This study only conducted fieldwork during the peak of the populations year-round breeding season (August to December) and although body condition was not significantly associated with

date (Julian day) within this peak period, studying Red-billed Tropicbirds breeding across the whole annual cycle would offer further insights into body condition regulation.

Many seabirds, including some tropicbird species, show a marked seasonality in breeding phenology, the onset of which is planned to coincide with the change of upwelling and marine productivity (Castillo-Guerrero, Guevara-Medina and Mellink, 2011). This is to ensure that the period of highest food demand during the chick rearing period is well-matched to the peak in food availability and enabling adult body condition to be maintained despite the demands of chick provisioning (Lack, 1968). Tropicbirds at St Helena showed no significant year-to-year variation in body condition across the incubation and chick rearing period suggesting that availability of prey early in the peak season may be high to relatively stable. In times of food shortage, birds can generally respond by reducing clutch and/or egg size to reduce the required energy intake (Drent and Daan, 1980; Birkhead and Nettleship, 1982), however as tropicbirds lay a single egg, they may instead respond by not breeding, or by delaying breeding until environmental conditions are more favourable. Our findings suggest that there may be a body condition threshold when deciding to breed, adults may need to reach a certain body condition before initiating a breeding attempt to balance the cost of reproductive effort against an individual's long-term survival. This is further supported by the increase in body condition prior to breeding as a buffer against loss of body reserves across the breeding attempt, a common strategy in pelagic seabirds (Cherel, Charrassin and Handrich, 1993).

4.6.2. Reproductive performance

This study found no relationship between reproductive performance and body condition a) during the incubation period, b) between incubation shifts, (despite their variable duration, ranging from <1 to 12 days), and c) during the chick rearing period. There was also no evidence that parental attendance during chick rearing influenced fledging outcome, supporting the findings in Chapter 2 during the same study period on St Helena, that significant between year variation in fledging success was driven by large between-year variations in daily chick survival due to high levels of chick predation. Indeed, our study indicates that Red-billed Tropicbirds can sustain body condition sufficiently to maintain their reproductive effort.

4.6.3. Sex-specific incubation routine

This is the first study to describe significant sex differences in incubation routine in Red-billed Tropicbirds, although it is not uncommon in other seabirds (Phillips, 1987; Chaurand and Weimerskirch, 1994; Weimerskirch, 1995; Pinet *et al.*, 2012). Such sex differences reflect different reproductive roles, the male takes the first long incubation shift so that the female can recuperate body condition after laying the egg. As a consequence, males tend

to have longer incubation shifts on average than females. Subsequently (after the first shift) incubation shifts changed in duration over the incubation period in a similar way in both males and females. The shorter incubation shifts observed closer to hatching suggests that Red-billed Tropicbirds adjust the length of time spent at sea foraging and therefore the incubation shift length to ensure that when the chick hatches, the attending adult can feed the chick before its yolk reserve runs out. This foraging trip regulation strategy is common in pelagic seabirds with extended incubation periods and long incubation shifts (Weimerskirch, Jouventin and Stahl, 1986; Johnstone and Davis, 1990; Nam, Kwon and Yoo, 2008; Gaston *et al.*, 2014) and there are three mutually non-exclusive hypotheses proposed to explain what could trigger this reduction in incubation shift length during the end of the incubation period; 1) endogenous timing, where adults can predict the timing of hatching, 2) response to embryo signals such as heart beat, or bill tapping providing a cue for parents to assess embryo development, and 3) that the declining incubation shift durations towards hatching is a consequence of a seasonal increase in food availability (González-Solís, 2004). Our data did not allow us to elucidate the underlying mechanisms for the reduction in incubation shift lengths close to hatching. It was also not possible to evaluate the level of synchrony within pairs during the incubation routine as not all incubation shifts for each pair and each nest could be identified. However, if I exclude the first shift, the results show similar consecutive shift lengths for the two sexes, suggesting a level of synchrony. Given that there was little evidence of differences in body condition between Red-billed Tropicbird sexes through the incubation and chick rearing periods or in the proportion of mass lost per day during incubation, females and males likely have similar reproductive efforts and resulting impacts on their body condition.

4.6.4. Body condition regulation

The significant decrease in body condition across the incubation period seems to be in part mitigated by the higher body condition observed in pre-breeding adults, suggesting that improved pre-breeding body condition may help to meet the demands of breeding such as laying the egg in females, ensuring there are sufficient body reserves to fast during incubation, and provisioning of food to the growing chick. The finding that adults with greater body condition are also able to undertake longer periods of fasting whilst incubating supports this hypothesis. Body condition generally decreased through incubation shifts, which adults presumably then attempt to replenish on the subsequent foraging trip. However, this is not always possible in seabirds, for example in male and female Streaked Shearwaters (*Calonectris leucomelas*) despite having similar mean incubation shift lengths, only male body condition decreased throughout the incubation period which was attributed to subsequent foraging trip performance (Nam, Kwon and

Yoo, 2008). Given the observed overall negative effect of the incubation period on body condition in both sexes, adults in our study may not be completely successful in regaining body condition, also indicating that both sexes may have similar foraging behaviour in subsequent foraging trips.

This study shows that Red-billed Tropicbirds can regulate energy expenditure (mass loss) regardless of the length of shift. Some seabird species are known to exhibit an initial drop in the rate of mass loss during the beginning of an incubation shift due to the stomach contents from the last meal being rapidly digested during the first few days of a fast (Henri Weimerskirch, 1990). In other species, the daily mass loss can vary throughout a fast, for example Emperor Penguins (*Aptenodytes forsteri*) (Groscolas, 1988). Red-billed Tropicbirds at St Helena show a constant rate of mass loss through incubation shifts in both sexes, the amount of which is influenced by how much of the incubation shift has been completed. Although the incubation shift length and incubation period did not significantly affect the proportion of mass lost per day, they were likely to have some effect overall as they were included in the final model. This model indicates that the further adults are into the incubation period, the rate of mass loss increases, suggesting that a Red-billed Tropicbird's ability to regulate body condition decreases during the incubation period.

4.6.5. Parental attendance during the chick rearing period

The high adult attendance rate identified during the first two weeks of life when adults brood and guard the chick are consistent with similar findings in Red-billed Tropicbirds on nearby Ascension Island (Stonehouse, 1962) and Red-tailed Tropicbirds in the Indian Ocean (Fleet, 1974; Diamond, 1975). The observed differences in parental attendance of the chick between Ascension and St Helena may be a consequence of the different time periods studied (Figure 4.7). There may also be different environmental influences on attendance due to the different geographical regions; Ascension is closer to the equator and generally warmer (Ascension Island sea surface temperature; range 24 to 28°C (Hughes, 2013), St Helena; 20 to 26°C (Cowburn *et al.*, 2021) and therefore on Ascension parents may not need to brood over chick for as long to ensure adequate thermoregulation of the chick in the nesting cavity. Interspecific competition with other seabird species, particularly White-tailed Tropicbirds (*Phaethon lepturus*) (Stonehouse, 1962) at Ascension may also cause parents to be less attentive to chicks overall than St Helena where Red-billed Tropicbirds only have to deal with intraspecific competition (AB pers. obs.). If we consider parental attendance up to a nesting age of 50 days, then attendance on parents on Ascension (53%, Stonehouse (1962)) and St Helena (66%) are

similar, compared to the much higher attendance of 83% observed in the Galapagos in 1965-67 (M. P. Harris, 1969).

4.6.6. Chick growth

The Red-billed Tropicbird growth rate of 6.6 g/day from St Helena and 8.4 g/day at Cabo Verde described here provides a baseline for comparison for future studies. The maximum mean chick mass observed on St Helena appears to be very similar to values previously reported from nearby Ascension Island (maximum mean mass 780g; Stonehouse, 1962), but larger than on Cabo Verde during the same season. It is not uncommon for tropicbird chick maximum mass, prior to fledging to be greater than that of adults (Diamond, 1975; Phillips, 1987) or for chicks to lose mass prior to fledging (Stonehouse, 1962; Medeiros, 2008). The observed large daily fluctuations in chick mass are likely due to adult attendance and provisioning effort, particularly for one chick from St Helena which showed periodic weight declines where presumably its parents were limiting provisioning frequency and amount. Such fluctuations were not as apparent at Cabo Verde, possibly due to the difference in frequency of data collection (every ≤ 5 days, as opposed to 2 days at St Helena) and limited monitoring during the first two weeks after hatching, when the highest rates of chick growth occur. As with many seabirds, tropicbirds are known to adjust chick food provisioning depending on food availability (Ramos and Pacheco, 2003), which can in turn affect development (Schaffner, 1990) and ultimately chick survival. Despite similar growth rates between regions, the fledglings in our study were heavier and structurally bigger at St Helena than at Cabo Verde (Table 4.5, Figure 4.8), likely representing a geographical variation in body size among Atlantic populations of Red-billed Tropicbirds, as shown for other tropicbird populations (Le Corre and Jouventin, 1999). These results agree with previous suggestions that phenotypic variation in adult body size among Red-billed Tropicbird colonies in the Pacific Ocean are primarily driven by phenotypic plasticity and responses to local environmental conditions, rather than genetic variation among colonies (Piña-Ortiz *et al.*, 2022).

Only one of the 12 St Helena chicks studied in 2017 failed to fledge. The failure cause was due to predation rather than poor development or attendance related reasons, therefore due to their success, the growth rates identified are likely to be at the higher end of the range, and I speculate that food availability may have been relatively stable in 2017 for this to occur. Inter-specific competition between seabird species may also be a factor affecting chick growth at Cabo Verde; two of the chicks in this study were recorded as being attacked by Cabo Verde Shearwaters (*Calonectris edwardsii*) which compete for nesting burrows with Red-billed Tropicbirds on Raso Islet (S. Saldanha *pers comm.*). The level of post-fledging care provided by Red-billed Tropicbirds remains relatively little

studied, although Ainley, Spear and Boekelheide (1986) suggested that parental care in tropicbirds may extend beyond departure from the nesting colony. The chicks that I studied on St Helena fledged with a final body mass not significantly smaller than adult mean body mass. This implies that chicks may have fledged with little to no food reserves, suggesting that they fledged before reaching mean adult size. It is advantageous for Red-billed Tropicbirds to provide post-fledging care, given its positive relationship with fledging survival probability (López-Idiáquez *et al.*, 2018).

4.6.7. Conclusions

This study identified between-year differences in body condition and impacts of these differences on the incubation regime of Red-billed Tropicbirds at St Helena. Although our study didn't formally test for such an association, our findings are the first to indicate an apparent influence of the Angola-Benguela upwelling system and the South Equatorial Current on reproduction and foraging behaviour of seabirds in the South Atlantic, although possibly less severe than the dramatic effects on seabird survival and reproduction documented for El Niño and decadal oceanographic oscillations (see Champagnon *et al.*, 2018). These results highlight the importance of multi-year studies and the need for further exploration of the impact of the Angola Benguela upwelling cycle on species and ecosystems.

Our results also provide new insights into the regulation of body condition across the breeding cycle in a pelagic seabird in the South Atlantic. In our study, Red-billed Tropicbirds at St Helena demonstrated flexible sex specific incubation regimes that were related to reproductive role. Despite variation in body condition in some years, reproductive performance was not affected, indicating that Red-billed Tropicbirds are able to mitigate loss of condition in years when food availability is likely to be relatively low. The flexibility and adaptability of body condition regulation in this pelagic species described here will be particularly important for threatened populations to optimise resources as global climate change and its effects on the marine environment influence prey availability.

Chapter 5.

Contrasting foraging strategies of two seasonally segregated populations of the South Atlantic Storm-petrel

This chapter is in preparation for submission for publication.

5.1. Abstract

Understanding the foraging ecology of the South Atlantic Storm-petrel (*Hydrobates helena*) is important for its conservation management. This study reports on the first multi-year GPS tracking of the two seasonally segregated populations of *H. helena* from their largest known breeding colony. A total of 44 GPS tags were deployed across two hot and two cool breeding seasons, spanning the incubation and chick rearing phases. This yielded tracking data of 23 short trips (mean duration $\pm$ SD: 8.4 ± 5.5 hrs, mean maximum range 28.43 ± 19.78 km from the colony) and 52 long trips (103.5 ± 62.8 hrs, 471.79 ± 303.46 km). No adverse impacts of tags were observed on adult body mass or nest survival rates. Long trips lasted up to 9 days and covered distances of up to 3,285km. The trip durations and distances were similar between the two seasonal populations, but trip direction differed markedly, resulting in pronounced seasonal differences in marine distributions: cool season breeding adults foraged across a larger area ($\sim 620,000\text{km}^2$) to the southeast of St Helena, while hot season breeding adults used a considerably smaller area ($\sim 400,000\text{ km}^2$) to the southwest. Oceanographic and climatic conditions influenced foraging locations during each season, with cool season breeders favouring cooler foraging locations than hot season breeders. Both seasonal populations consistently foraged beyond the 200km radius of the St Helena Marine Protected Area (MPA), highlighting that existing MPA size is insufficient to encompass the observed breeding season foraging ranges of the species that the MPA was designated to protect. Hot and cool season populations of *H. helena* have been previously shown to lack clear genetic differentiation. Their strong foraging range segregation identified in this study is therefore consistent with previous suggestions that at-sea distribution is a driver of sympatric speciation in seabirds.

5.2. Introduction

In tropical oceans, productivity is low compared to temperate and polar waters (Longhurst and Pauly, 1987), and seabird prey distribution is patchy (Ashmole, 1971; Weimerskirch, 2007). Consequently, in this highly oligotrophic environment, seabirds often associate with

local areas of higher productivity such as seamounts and fronts between different water bodies (Thiers *et al.*, 2014), or associate with the distribution and foraging activity of sub-surface predators (Harrison *et al.*, 1991; Ballance, Pitman and Reilly, 1997). Several distinct foraging strategies may exist within a given seabird population, reflecting a combination of behavioural, environmental and physical drivers resulting from differences among individuals, life history or state variables such as age, sex or breeding stage (McNamara and Houston 2007, Phillips *et al.*, 2017). For example, during chick rearing many seabirds will change their foraging strategy to balance the differing energetic requirements associated with provisioning offspring versus self-provisioning, often forcing parents to forage closer to the colony which chick provisioning than in any other breeding stage (González-Solís, Croxall and Afanasyev, 2007; Phillips *et al.*, 2007).

Highly pelagic seabirds, such as those within the order Procellariiformes (albatrosses, petrels and shearwaters) often exhibit extreme life history traits such as long life spans, low fecundity, long chick rearing periods and high nest and mate fidelity, thus reducing their adaptability and increasing their vulnerability to threats imposed by environmental change (Warham, 1990). Different species of pelagic seabirds are also known to exhibit substantial differences in patterns of space use at sea, warranting alternative conservation management approaches (Oppel *et al.*, 2018). Understanding species distribution and activity patterns is essential to assist in the identification of threats that may have conservation implications for species. Consideration of how species utilise the marine environment in the context of their ecological and life history traits will help inform long term management and conservation of such species, through appropriate spatial planning such as designation of Marine Protected Areas (MPAs) (Oppel *et al.*, 2018; Bolton, 2020).

Identifying management units for species conservation is typically challenging, especially for populations where there is taxonomic uncertainty (Godfray, Knapp and Mace, 2004; Coates, Byrne and Moritz, 2018). The mechanisms of population differentiation and speciation in seabirds are complex. Speciation typically occurs where geographical barriers to dispersal affect gene flow between populations (Friesen, Burg and McCoy, 2007), but can also occur when, as an adaptive response to environmental conditions, populations separate by breeding time ("allochrony") and the seasonal populations become reproductively isolated e.g., Band-rumped Storm-petrels (*Hydrobates castro*) in the Galapagos Islands (Smith and Friesen, 2007) and the Azores (Monteiro and Furness, 1998; Bolton *et al.*, 2008). The foraging range(s) of a species can also influence the genetic structure of populations; e.g., geographically separate populations of Black-browed Albatross (*Thalassarche melanophrys*) with different foraging grounds differed genetically, despite a lack of physical barriers to dispersal between foraging areas where

mixing could occur (Burg and Croxall, 2001). Whether a species forages relatively close to the colony or forages offshore where the probability of encountering individuals from different populations, and therefore potentially breeding at other colonies, may be higher, could also influence gene flow and thus genetic structure of the population (Friesen, Burg and McCoy, 2007).

Previously, identification of marine distributions of small pelagic seabird species was reliant on visual observational data which could be restricted by weather conditions, species activity patterns and small size, influencing detectability. Other approaches included inferring ranges from stable isotope analyses e.g., Martinez *et al.*, (2019) or using light-based geolocation (Global Location Sensing; GLS logging), to allow identification of broad scale habitat preferences Phillips *et al.*, (2004). Until recently, fine-scale high precision tracking and characterisation of at sea distributions has only been possible for larger storm petrel species weighing >50g, e.g., Leach's Storm-petrel (*Hydrobates leucorhous*) (Pollet *et al.*, 2014; Halpin *et al.*, 2018). Studies are often limited by a combination of the size of the study species, device size (Phillips *et al.*, 2003) and the possible negative impact that even short-term handling or disturbance at the nest may cause (Blackmer, Ackerman and Nevitt, 2004; Kim *et al.*, 2014). The improved development and miniaturisation of reliable high resolution Global Positioning System (GPS) devices has created new research opportunities for species that were previously unattainable e.g., European Storm-petrel (*Hydrobates pelagicus*) (Bolton, 2020; Rotger *et al.*, 2020; Pascalis *et al.*, 2021), and rapidly advancing our understanding of species exposure to threats, populations, ecosystems and their interactions with resource availability and a changing environment (Kays *et al.*, 2015; Clark *et al.*, 2023). However, many storm petrel species and populations remain poorly studied and still lack comprehensive information on key aspects of foraging ecology.

The South Atlantic Storm-petrel (*Hydrobates helena*) is a little-known and newly designated endemic pelagic seabird species, geographically isolated in the South Atlantic Ocean, *H. helena* is only known to breed on two island groups; St Helena and Ascension Island, and their associated islets. The population is also reproductively seasonally isolated, breeding in two discrete periods: in the austral summer (late September to late December) and in the austral winter (Chapter 3, Bennett, Bolton and Hilton (2009)), hereafter, “hot season” and “cool season” respectively. Despite *H. helena* having seasonally segregated breeding populations that exhibit little to no temporal overlap (Chapter 3), the two seasonal populations show only limited differences in morphology and vocalisations (Bolton *et al.*, in prep) and are not sufficiently genetically differentiated from each other to be considered as cryptic sister-species within the *H. helena* taxon

Chapter 5: Foraging strategies and behaviour of South Atlantic Storm-petrel (*Hydrobates helena*) (Friesen *et al.*, 2007; Taylor *et al.*, 2019). Consequently, these seasonal populations are thought to be in the early stages of divergence but recognised currently as a single management unit for conservation.

The primary goal of this study was to provide detailed information on the at-sea breeding distribution and foraging ecology of *H. helena* in order to inform conservation management strategy and policy. I characterised the spatial ecology and foraging strategies of the two seasonally-segregated breeding populations of *H. helena* at Egg Island in St Helena, the largest known breeding colony in the South Atlantic (Bolton *et al.*, in prep) and tested for differences between seasons, breeding stages, years and sexes.

In this study, I address four main questions:

- 1) What are the foraging strategies of breeding *H. helena*? I predict that *H. helena* are nocturnal, predominantly active at the colony and foraging during the hours of darkness, mirroring other *Hydrobates* species (Thomas, Medeiros and Pollard, 2006; Poot, 2008; Medrano, Militão, *et al.*, 2022), and that the species will forage mainly offshore as opposed to close inshore (<10km) as observed in most other *Hydrobates* species (Oppel *et al.*, 2018).
- 2) Does marine spatial distribution and foraging habitat preferences differ between the seasonal populations of *H. helena*? If foraging distribution is primarily a fixed phenotypic trait, I predict that there is likely to be considerable spatial overlap in foraging distributions between the two seasonally-segregated populations, given their genetic connectivity (Taylor *et al.*, 2019). If however, foraging distribution is primarily a behavioural plastic response to seasonal conditions, then I predict that the two seasonally segregated populations may differ substantially in their foraging ranges.
- 3) Can any differences in foraging distribution between breeding seasons be explained by environmental conditions, through examining a range of oceanographic and atmospheric features? I predict that differences within and between years in environmental conditions and consequent prey availability, may affect foraging behaviour and distribution at sea (Pascalis *et al.*, 2021).
- 4) What is the spatial distribution, and consistency of distribution between seasons, in relation to the Marine Protected Area surrounding St Helena? This information is essential in order to assess the effectiveness of current protection measures, and to discuss the implications of my findings for the conservation and management of the species in the South Atlantic.

5.3. Methods

5.3.1. Study area

Fieldwork was carried out on Egg Island, a small islet off the north-west coast of St Helena in the South Atlantic Ocean. The islet has an established network of artificial nest chambers, readily used by both of the seasonally segregated breeding populations of *H. helena* (Chapter 3).

5.3.2. GPS tracking and data processing

Over three calendar years, encompassing two hot seasons (late September to late December in 2017 and 2018) and two cool seasons (late March to early July in 2018 and 2019), breeding *H. helena* were equipped with 0.95g GPS devices (NanoFix-GEO mini, Pathtrack Ltd, Otley, UK). GPS devices measured 20x10x4.5mm (NanoFix-GEO mini), plus a thin whip antenna (50mm long), and were attached to the four central rectrices (tail feathers) using three narrow strips of waterproof TESA Tape (Beiersdorf, Germany) for periods of 2-12 days. The mass of the device and attaching material weighed 1.1g, corresponding to 1.9-2.9% of the body mass of tagged birds at deployment and thus below the accepted 3% threshold associated with adverse impacts (Phillips *et al.*, 2003). To minimise the risk of nest-desertion and GPS loss I only tracked experienced breeding birds, known from ring numbers to have bred at least once before. GPS devices were set to record a position at 120-minute intervals during incubation, and 60-minute intervals during chick-rearing, however some ($n = 3$ deployments) initial settings used longer fixed intervals, to test battery life expectancy (Appendix 2, Table A2.2). Handling time was kept to a minimum, taking no longer than 10 minutes per bird. All tracked birds were weighed prior to device attachment, and again at recapture after device removal, then returned to their artificial nest chamber immediately after handling.

Location data from GPS loggers were downloaded using Pathtrack Archival GPS Logger software (V1.5, Pathtrack Ltd, UK). Inaccurate GPS locations were identified by visual inspection of each track and any spatially/temporally unrealistic points removed. Foraging trips were differentiated using the 'tripsplit' function in the *track2KBA* R package (Beal *et al.*, 2021) into those by adults attending the nest, during which the chick or egg was temporarily left alone ('short trips'), and those undertaken by the non-attending partner ('long trips'). Long foraging trips were further defined as a series of more than five locations travelling at least 20 km from the colony, returning to within 30km of the colony and lasting for more than 4 hours in duration. Foraging trip parameters (including the total distance travelled, maximum distance from the colony, and trip duration) were calculated using the 'tripdistance' function in the *trip* R package (Sumner, Wotherspoon and Hindell,

2009; Sumner, 2011). The total trip distance was calculated as the sum of all step lengths between subsequent locations assuming straight line travel between all position fixes, maximum trip distance as the most distant point from the colony along each trip and the total trip duration as the minimum time each trip took to complete (time difference between departure and return locations in the colony). To quantify the general direction in which foraging trips were orientated, I calculated the bearing from the colony to the most distant point along each foraging trip using the *circular* R package (Agostinelli and Lund, 2017).

Using GPS data, foraging behaviour during each long foraging trip was classified using first passage time (FPT); the time taken to depart a circle of a given radius (Fauchald and Tveraa, 2003) to identify regions of area restricted search (ARS). Each trip was converted to a trajectory and subsequent first passage time analyses were implemented using the 'as.ltraj' and 'fpt' functions respectively with the *adehabitatL* TR package (Calenge, 2006a). Individual ARS values were calculated and the peak in the variance of log (FPT) values for each independent trip were used to define a mean search scale for the population, of 6th radius = 0.05. Locations where the FPT value was higher than the mean FPT value across all trips (i.e., > 1.0) were taken to be foraging rather than travelling.

5.3.3. Statistical analysis

All statistical analyses were carried out in the statistical program R 3.5.1 (R Development Core Team, 2021). All generalised linear mixed models (henceforth GLMMs) were implemented in the *lme4* package (Bates *et al.*, 2015) using the 'glmer' function, all correlation, *t*-tests and GLMs in the *stats* package (R Core Team and contributors worldwide, 2021), all likelihood-ratio tests (LRTs) in the *lmtest* package (Zeileis and Hothorn, 2002) and all generalised additive mixed models (henceforth GAMMs) in the *gamm4* package (Wood and Scheipl, 2020), following Thomas *et al.*, (2017). Calculations of conditional and marginal R² values for GLMMs were completed using the 'r.squaredGLMM' function in the *MuMIn* package (Barton, 2020). All circular ANOVAs were generated using the 'aov.circular' function in the *circular* package (Agostinelli and Lund, 2017). Checks for data collinearity were implemented using the 'check_collinearity' function in the *performance* package (Lüdtke *et al.*, 2021). Significant effects in all final models were plotted using the *ggplot2* R package (Wickham, 2016).

5.3.3.1. Effects of tag attachment

A paired *t*-test was used to examine any differences in mass at deployment and retrieval, across all tracked individuals. I concluded that devices did not adversely affect tracked birds if body mass after tracking did not significantly differ ($P \geq 0.05$) from body mass when the tag was fitted. In addition to all nests in artificial nest chambers with tracked

birds, an equal number of randomly selected control nests ($n = 34$) were monitored each season to evaluate the effect that GPS devices may have on breeding success. Daily egg and chick survival rates $\pm 1\text{se}$ were calculated following Mayfield (1975) and Johnson (1979), assuming incubation and chick-rearing periods of 42 and 70 days, respectively (Allan, 1962; M. Harris, 1969). I constructed two logistic exposure GLMMs (Shaffer, 2004; Bolker *et al.*, 2009) to assess if hatching or fledging success and productivity varied between nests that were used to track breeding adults and control nests. One model contained just the response variable: either hatching success, fledging success or productivity (null model) and the other with the addition of tracking as a binomial (yes/no) fixed factor. Season and year were used as random effects to control for temporal variation. I then used LRTs to compare the models to null models and concluded that tracking was a significant influence on hatching or fledging success if $P < 0.05$.

5.3.3.2. Foraging trip parameter analysis

To examine whether mean foraging trip direction varied between sexes (male vs. female), breeding stages (incubation vs. chick rearing) or seasons (hot vs. cold), a series of circular ANOVAs were used (Pewsey, Neuhauser and Ruxton, 2013). Differences in other foraging trip parameters were examined, using GLMMs with individual identity (ID) nested within year as a random effect to account for non-independence between multiple trips by the same individual (a potential source of pseudo-replication) and any variation in foraging distances between the different years in which birds were tracked. Breeding stage (Sommerfeld and Hennicke, 2010; Weimerskirch *et al.*, 2010), season (Le Corre *et al.*, 2003; Markones, Dierschke and Garthe, 2010; Oppel *et al.*, 2017) and sex (González-Solís, Croxall and Wood, 2000; Lewis *et al.*, 2005; Hennicke, James and Weimerskirch, 2015) are each known to affect the foraging range of many seabird species, and therefore they were used as fixed effects in models as well as the other variables of interest. For each foraging trip parameter, as a normally distributed response variable, I constructed two GLMMs. One model containing the fixed effects (sex, season and breeding stage), then the second model without the variable of interest (null model) but including the same other fixed effects. Using a LRT I compared models to null models which lacked the variable of interest. If the LRT statistic was significant at $P < 0.05$, I interpreted the results as evidence for significant effects and examined parameter estimates to quantify these effects. As initial analyses revealed that total distance travelled, total trip duration, and maximum foraging trip distance on short trips, did not vary by sex or season (LRT all $P > 0.1$, $n = 14$ trips for males, $n = 9$ for females), data from all short trips were pooled for comparisons with long trips.

5.3.3.3. Assessing variation in foraging behaviour

To investigate if foraging behaviour also differed between seasons, breeding stages and sexes, I divided each trip into two hourly intervals and estimated the proportion of time spent foraging, identified by the FPT analysis. I weighted this parameter with the total number of two hourly intervals in which data was recorded per trip. Three binomial GAMMs were then performed, in which the binary response (foraged: true/false) was modelled as a function of time, (treated as a smoothed term using a cyclic cubic spline (Wood and Scheipl, 2020) following Thomas *et al.*, (2017), with the variable of interest (season, breeding stage or sex). To account for repeated measures of individuals, individual identity (ID) was included as a random effect along with deployment ID nested within year as a random effect in each model to account for variation in the likelihood of foraging during different time periods and multiple trips within each year. Significant effects ($P < 0.05$) were plotted.

5.3.3.4. Spatial distribution and seasonal shifts in utilisation

To quantify the marine spatial distribution of *H. helena* from St Helena, and to assess whether the size of the utilisation distributions differed between seasons kernel utilisation distributions were calculated using the *adehabitatHR* package (Calenge, 2006b). Specifying a 1x1km grid resolution, the "kernelUD" function was used to estimate the 95%, 75% and 50% kernel utilisation distributions (henceforth KUDs) of all locations associated with long trips. The kernel smoothing parameter was defined using the ad hoc method (Kie, 2013) whereby the reference bandwidth (h_{ref}), calculated using the 'findscale' function in the track2KBA package (Beal *et al.*, 2021) is slowly reduced in increments until a single contiguous 95% home range is achieved. This process was done for all long trips (combined seasons, years and breeding stages) to arrive at a bandwidth value of 44km that was used across both seasons and stages. First, I examined the general (95%) and core (50%) UD for the whole population of *H. helena* in relation to the MPA, then I examined whether KUDs varied between seasons, and compared each season to the MPA. The kernel overlap between the two seasons and between years for each season were quantified using the Bhattacharyya's affinity index (BA), estimated by means of the "kerneloverlap" function. This is a non-directional statistical measure of affinity that ranges from 0 (no spatial similarity between distributions) to 1 (identical spatial distributions), and is considered the most appropriate index for quantifying the similarity between utilization distributions (Fieberg and Kochanny, 2005; Wakefield *et al.*, 2015).

5.3.3.4. Analysis of environmental relationships

To explore whether *H. helena* shifted their spatial distribution when foraging in response to environmental variation, I considered a number of oceanographic and atmospheric

variables, downloaded from the Env-Data system in Movebank (Dodge *et al.*, 2013), corresponding both spatially and temporally to the tracking data (Appendix 2, Table A2.3). Wind speed (m/s) and direction (degrees) were computed at each location from surface wind vectors (zonal and meridional velocities, 0.75 degree resolution, daily European Centre for Medium-Range Weather Forecasts (ECMWF)). Surface current vectors (zonal and meridional velocities, 0.33 degree resolution, five days Ocean Surface Current Analysis Real-time (OSCAR)) were combined to calculate current speed (m/s). To test for correlation between environmental variables, all variables were standardised prior to testing. Variables were deemed highly correlated if $r_s > 0.5$ (Appendix 2, Table A2.4; wind speed and wave direction, air temperature and sea surface temperature). Wave direction and air temperature were then removed as they made less ecological sense than their counterpart. I then fitted a GLM with 'logit' link binomial error distribution to the dependant variable; foraging (yes/no), identified from the FPT analysis. Environmental covariates were fitted as independent variables, and variance inflation factors (VIF) were examined for the fitted model, some environmental variables that were strongly correlated were then excluded using a threshold of $VIF \geq 5$ to minimise collinearity.

To examine whether *H. helena* also shifted their spatial distribution seasonally in response to environmental variation, I fitted two GLMMs to each environmental variable as a gamma response and a 'log' link function. I first examined whether foraging on a trip was unrelated to the season (null model) then whether the environmental conditions where they foraged varied by each season. Trip ID was nested within year as a random factor, to account for any variation between years and non-independence of locations along a long trip. Individual ID was also used as a random factor to account for multiple trips by individuals. As none of the environmental variables investigated varied with breeding stage (GLMM < all $P > 0.1$, $n = 2196$ locations for incubating adults and 410 locations for chick rearing adults), data from both breeding stages were pooled for comparisons between seasons. A LRT was then used to test for the significance of the independent terms in the model (Lewis, Butler and Gilbert, 2011). To assess the explanatory power of the full model, I calculated how much of the variance in the dependent variable was explained by the environmental variable in the model (conditional R^2) modified from (Nakagawa and Schielzeth, 2013).

To compare the foraging locations that storm-petrels used in a given season to those that they could have used (based on foraging locations in the other season), I additionally requested the same oceanographic and atmospheric variables from the Env-Data system in Movebank (Dodge *et al.*, 2013) from potentially 'available' locations. I defined these available locations as the foraging locations from the opposite season and extracted the

environmental conditions at these 'available' locations by randomly assigning date and times from the actual foraging locations to the 'available' locations. The differences in mean environmental conditions between foraging locations used by cool and hot season birds were compared using non-parametric Mann-Whitney tests. Comparisons were also made between the foraging locations used and the 'available' locations for each season. 95% confidence intervals were calculated using a bootstrap procedure iterated 1000 times (Hall, 1992). Values are given as mean $\pm$ SD unless stated otherwise.

5.4. Results

Fifty-four GPS loggers were deployed on *H. helena* on Egg Island; 47 birds were recaptured, one retrieved bird had lost the logger, one retrieved logger failed to record, and one bird had not left its nest during the deployment, thus I retrieved 44 loggers with usable trip data (Appendix 2; Table A2.2, Figure A2.1). Seventy five foraging trips were distinguished; 52 long trips and 23 short trips. Departures from the colony occurred at almost all hours (Appendix 2; Figure A2.2, mean 0:39am) with the majority of adults returning around the hours of dusk (mean 08:05pm).

5.4.1. Effects of tag attachment

One individual lost all four central rectrices and the attached GPS logger. All other attached loggers were intact upon recovery; however, three individuals lost 1-2 central rectrices after removal of the logger and tape. Breeding adults during the cool season were significantly heavier ($t_{402.63} = -2.8578$, $P = 0.004$, $n = 417$) by on average 2g than hot season breeding adults (cool: 49.09 ± 4.89 g, $n = 219$, hot: 47.67 ± 5.26 g, $n = 198$). Across both seasons, adult body mass was not significantly different between logger deployment and retrieval ($t_{44} = 0.923$, $P = 0.361$, $n = 45$) despite decreasing by an average of $0.79 \pm 6.86\%$ (0.49 ± 3.55 g) whilst being tracked. There was no significant difference in hatching success (LRT $\chi^2_4 = 0.2455$, $P = 0.620$), fledging success (LRT $\chi^2_4 = 1.0625$, $P = 0.303$) or overall productivity (LRT $\chi^2_4 = 0.3551$, $P = 0.551$) between control nests and those that were used to track adults (Appendix 2, Figure A2.3). I therefore conclude that overall the GPS tracking technique did not adversely affect breeding *H. helena*.

5.4.2. Short Trips

A total of 23 short trips made by 14 individuals were identified during the study, occurring predominantly during the cool season (Table 5.1). Typically, the adult on incubation duty left the nest at dawn, leaving the egg unattended for the majority of daylight hours (mean 8.39hrs, range 2-18hrs), and then returned at dusk. All of these short trips were within the 200 nautical mile (nm) MPA, extending no further than 47.13nm (87.28km) and centred in

a westerly direction from the colony (mean $\pm$ SD $271 \pm 71^\circ$) on the leeward side of the island (Figure 5.1). Short trip direction did not differ between seasons (circular ANOVA $F_1 = <0.001$, $P = 0.993$) but differed significantly between sexes (circular ANOVA $F_1 = 7.972$, $P = 0.010$), with females foraging in a SSW direction (mean $222 \pm 88^\circ$ SD, $n = 9$) whereas males foraged towards WNW (mean $303 \pm 31^\circ$ SD, $n = 14$).

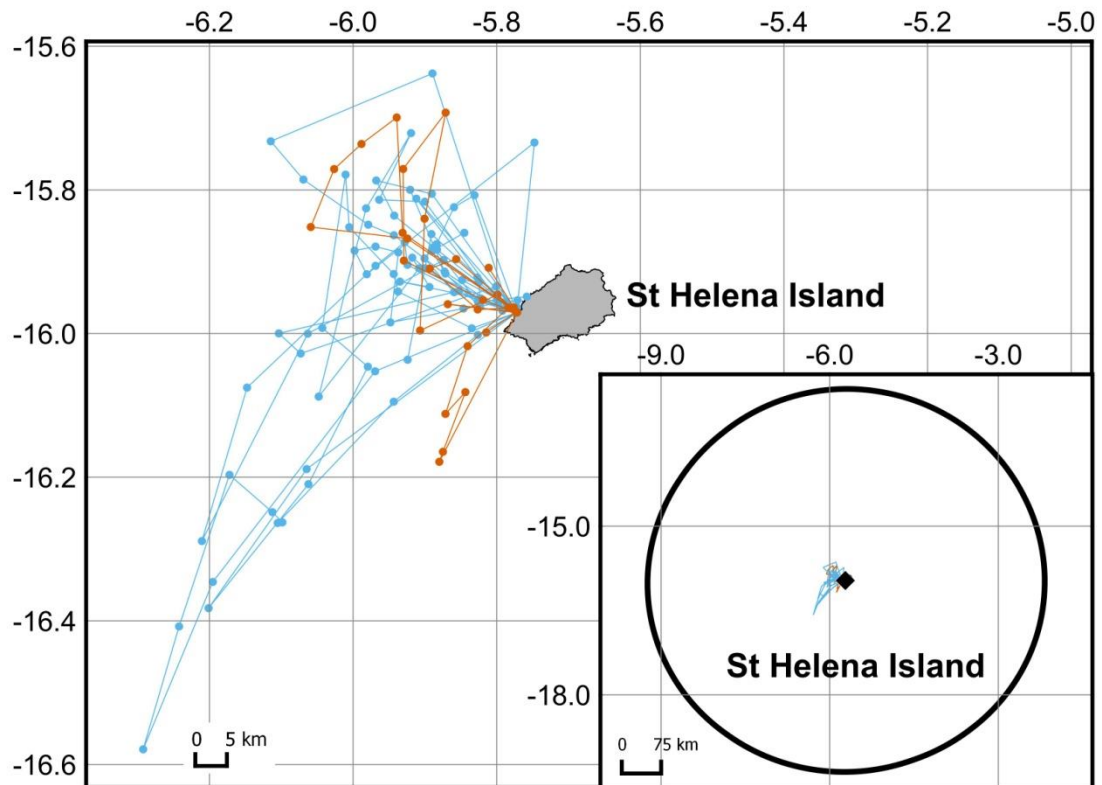


Figure 5.1. Short foraging trips made by incubating South Atlantic Storm Petrels during the cool (blue) and hot (orange) season from St Helena. The insert shows these short trips in relation to the 200 nautical mile MPA (black circle) around St Helena (black diamond).

Table 5.1. Mean, SD, minimum (min) and maximum (max) trip characteristics of 37 individual South Atlantic Storm-petrels (*Hydrobates helena*) tracked with GPS loggers, grouped by trip type, season and breeding stage. See Table 5.2 for significance values.

Trip characteristic													
Season	Breeding stage	N birds	N trips	Short Trips									
				Trip duration (h)			Max distance from colony (km)			Total trip distance (km)			Direction
				Mean $\pm$ SD	Min	Max	Mean $\pm$ SD	Min	Max	Mean $\pm$ SD	Min	Max	Mean
Hot	Incubation	5	7	7.57 $\pm$ 5.83	2.00	16.00	18.82 $\pm$ 12.15	5.51	35.04	46.84 $\pm$ 36.58	10.95	95.07	265 $\pm$ 79°
Cool	Incubation	9	16	8.75 $\pm$ 5.56	2.00	18.00	32.64 $\pm$ 21.29	9.53	87.28	77.51 $\pm$ 54.62	19.45	188.56	285 $\pm$ 49°
Long Trips													
Hot	Incubation	16	20	136.00 $\pm$ 46.94	10.00	232.00	531.25 $\pm$ 255.04	25.82	873.09	1726.89 $\pm$ 727.71	58.01	3285.02	215 $\pm$ 0.78°
	Chick Rearing	1	4	38.25 $\pm$ 37.36	17.00	94.00	269.05 $\pm$ 292.09	82.40	697.79	619.06 $\pm$ 623.88	237.26	1542.20	74 $\pm$ 3.77°
Cool	Incubation	17	18	117.44 $\pm$ 57.92	10.00	212.00	587.47 $\pm$ 305.72	26.65	1043.68	1831.13 $\pm$ 971.25	59.08	3227.63	131 $\pm$ 0.92°
	Chick Rearing	3	10	39.50 $\pm$ 41.34	5.00	138.00	225.74 $\pm$ 243.71	43.56	740.55	615.48 $\pm$ 698.31	94.76	2242.93	76 $\pm$ 2.67°

5.4.3. Long trips

The furthest a storm petrel travelled in one trip was over 3285km, the longest trip lasted over nine days and the furthest distance recorded from the colony was 1043km (563nm) (Table 5.1, Figure 5.2A). After accounting for differences between sex (male or female), season (hot and cool), repeat trips by individuals within a year and multiple years, the models revealed differences between breeding stages in foraging trip duration, total distance travelled in one trip and maximum distance travelled from the colony (Table 5.2). In contrast, there were no sex and season differences in these trip characteristics (Table 5.2). Individuals incubating an egg undertook foraging trips on average 88 hours (3.67 days) longer (127.21 ± 53.54 , range 10-232 hrs) covering 1159.8km further (mean 1776.27 ± 841.51 , range 58-3285km) and extended an average additional 319.8km (mean 557.88 ± 277.76 , range 26-1044km) from the colony than those rearing a chick (mean duration 39.14 ± 38.79 , range 5-138 hrs, mean total trip distance 616.5 ± 653.8 , range 95-2243km, mean maximum distance 238.1 ± 247.4 , range 44-740km) (Table 5.1, Appendix 2, Figure A2.4). Foraging trips occurred in nearly all directions when pooled across seasons, sexes and breeding stages (Figure 5.2B) with a mean southerly direction of 178° . There were no differences in the mean foraging direction between sexes ($F_1 = 0.091$, $P = 0.764$) or breeding stages ($F_1 = 0.796$, $P = 0.376$), however foraging trips during the cool season were on average in a south easterly direction (mean $130 \pm 87^\circ$ SD, $n = 28$), differing significantly from a south westerly direction in the hot season (mean $\pm$ SD $215 \pm 70^\circ$, $n = 24$, °; $F_1 = 20.05$, $P < 0.001$, Figure 5.2B).

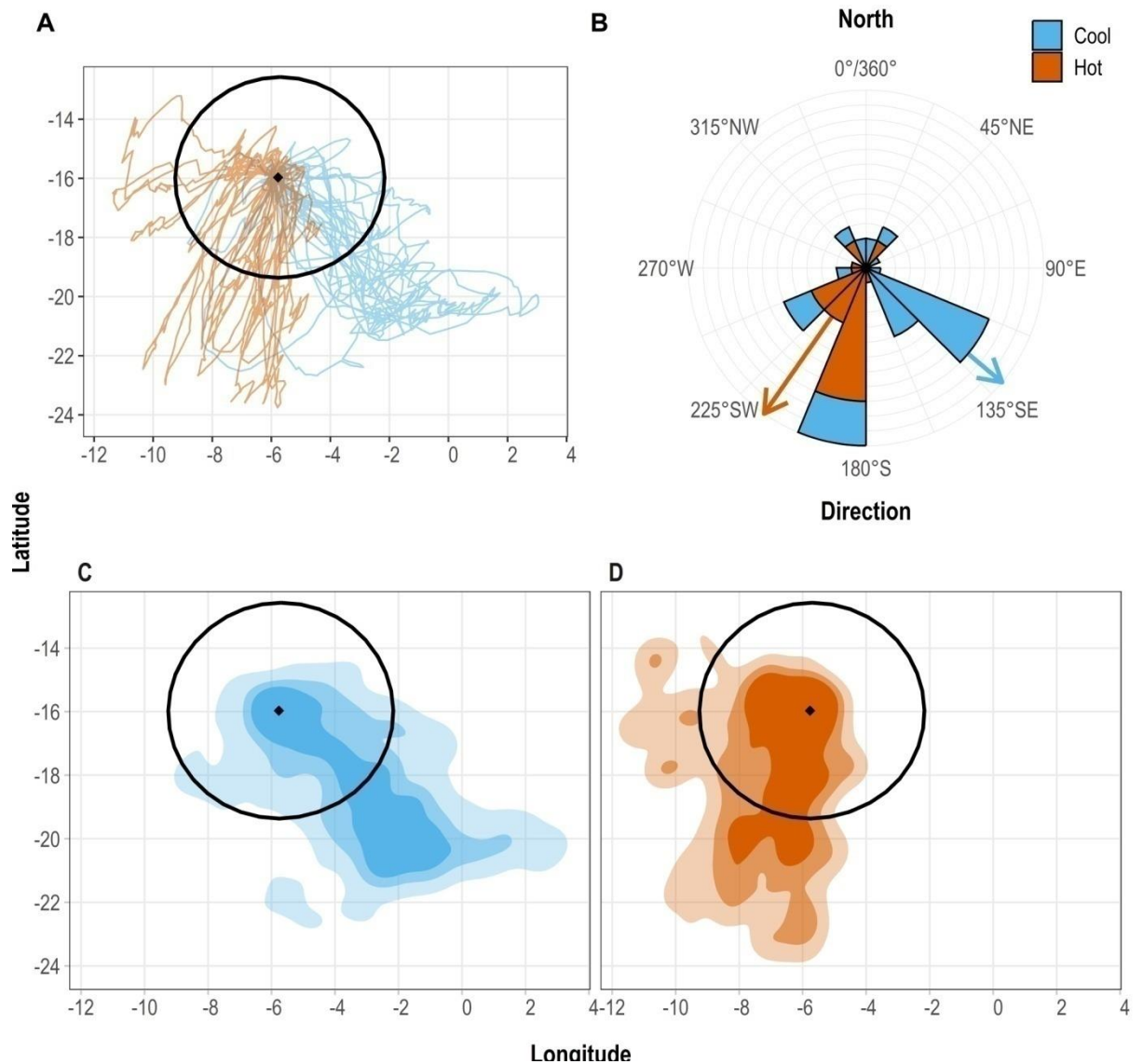


Figure 5.2. Long foraging trips of South Atlantic Storm Petrel (*H. helena*) ($n = 52$) tracked with GPS from St Helena between 2017 and 2019 during the cool (blue) and hot (orange) breeding season. **A)** Distribution of foraging trips for the hot and cool seasons that were used to calculate kernel utilization distributions (KUDs). The black diamond indicates the location of St Helena Island and the black line indicates the 200 nm Marine Protected Area (MPA). **B)** Frequency of foraging trip direction by season. Arrows indicate mean trip direction per season. Height of segments reflects the number of trips going into each 22.5 degree segment. **C & D)** The 95, 75, and 50% KUD, respectively, during the C) cool season (blue, bottom left panel) and **D)** hot season (orange, bottom right panel).

Table 5.2. Effect of season (cool and hot), sex (male or female) and breeding stage (incubating or chick rearing) on trip characteristics of South Atlantic Storm-petrels (*H. helena*) from St Helena tracked with GPS loggers. Test statistics are provided with a *P* value, and significant differences between trip types are shown in bold. See Table 5.1 for parameter estimates.

Trip metrics	Season		Sex		Breeding stage	
	Statistic	<i>P</i>	Statistic	<i>P</i>	Statistic	<i>P</i>
Total distance travelled	$\chi^2_1 = 0.038$	0.846	$\chi^2_1 = 0.190$	0.663	$\chi^2_1 = 13.370$	<0.001
Maximum distance	$\chi^2_1 = 0.016$	0.900	$\chi^2 = 0.231$	0.630	$\chi^2_1 = 9.323$	0.002
Duration	$\chi^2_1 = 0.314$	0.575	$\chi^2_1 = 0.290$	0.590	$\chi^2_1 = 16.281$	<0.001
Direction	$F_1 = 20.05$	< 0.001	$F_1 = 0.091$	0.764	$F_1 = 0.796$	0.376

5.4.4. Spatial distribution and seasonal shifts

The 95% kernel utilisation distribution (KUD) of *H. helena* at St Helena during long trips covered 915,908 km², 2.04 times larger than the MPA, and extended in a general southerly direction (Appendix 2, Figure A2.5). Only 35.16% (322,012 km²) of the 95% KUD was within the MPA boundary. The core area characterised by the 50% KUD was 228,473 km²; of which 64.36% (147,054.1 km²) was within the MPA boundary.

The 95% kernel UD of all long trip locations during the cool season was 619.164 km² and centred to the south-east of St Helena (Figure 2.5C), while the 95% UD during the hot season was of a similar size (599,984 km²) but centred to the south-west (Figure 2.5D). Whilst the majority of the core area during the hot season (153,880 km²) was contained within the MPA boundary (73.58%, 113,227 km²), only 44.16% (65,185 km²) of the core area during the cool season (147,622.2 km²) was within the MPA boundary.

The two seasonal distributions had a moderate overlap, indicated by the Bhattacharyya's affinity index (BA index) of 0.502. There was considerable overlap in utilisation distributions within each season between years; the hot season overlapping extensively between years (2017 and 2018, BA = 0.811) compared to the cool season (2018 and 2019, BA = 0.670). The mean ($\pm$ SD) percent spatial overlap of UD's within years between the hot and cool season was $27.9 \pm 6.0\%$ and therefore much lower than the overlap between years within seasons ($55.1 \pm 11.6\%$, Appendix 2, Table A2.5).

5.4.5. Foraging behaviour in relation to breeding stage, season and sex

There was little evidence of overall differences in time spent foraging between the sexes (female mean 37%, male mean 38%, GAMM; $\chi^2_1 = 0.058$, $z = 0.240$, $P = 0.810$, $n = 624$) or breeding stages, despite adults during the incubation period spending on average 7% more time foraging than adults rearing chicks (average 39% vs. 32%, GAMM; $\chi^2_1 = 0.592$, $z = -0.769$, $P = 0.442$, $n = 624$). However, during the hot season adults spent on average 16% more time foraging on a long trip compared to adults during the cool season (average 46% vs. 30% time foraging, GAMM; $\chi^2_1 = 16.58$, $z = 4.071$, $P < 0.001$, $n = 624$, Figure 5.3).

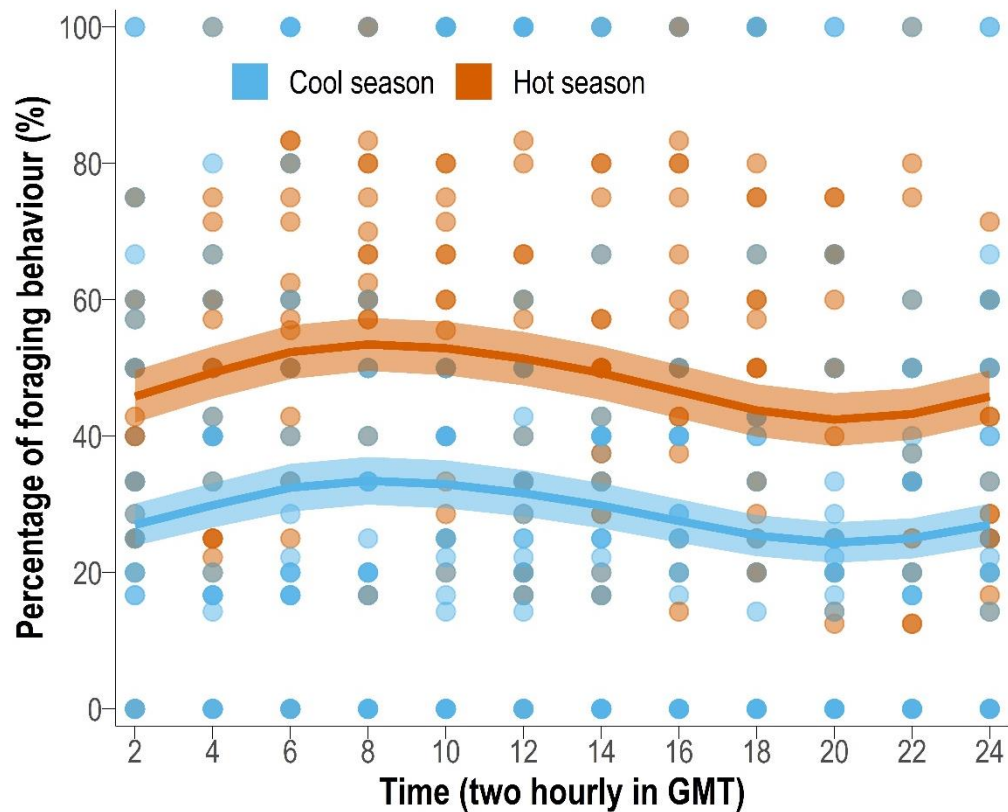


Figure 5.3. Proportion of foraging behaviour identified on long trips of *H. helena* at two hourly intervals through the day and night, during the hot (orange) and cool (blue) season breeding adults. For each season, the solid line represents the probability of foraging, and the shaded areas indicate $\pm 1SE$.

5.4.6. Environmental influences

After accounting for multiple long trips by individuals, any non-independence of locations along a long trip, variation in different time periods, seasons and breeding stages, the model that best explained variation in the probability of foraging included speed of current, sunshine duration, wave height, atmospheric water and sea level pressure (Table 5.3a, model 5, $R^2_{\text{marginal}} = 0.091$, $R^2_{\text{conditional}} = 0.217$). The final model indicated that *H. helena* were more likely to forage at locations with slow current speeds, high wave heights, under

more overcast conditions, and when there were low amounts of water in the atmosphere (Table 5.3b). Chlorophyll *a* concentration explained the least amount of variation in choice of foraging locations (Table 5.3a).

There was also strong statistical support for environmental differences in choice of foraging locations between seasons (Table 5.4). Hot season breeding *H. helena* adults foraged in lower sea surface temperatures, higher wind speeds, cloud cover and atmospheric water. This is in contrast to cool season breeding adults which foraged at locations with higher sea surface temperatures, lower wind speeds, cloud cover and atmospheric water (Table 5.4). Both seasonal populations had a preference for foraging in areas with increased wave heights and of low atmospheric water (Table 5.3b), but hot season adults significantly preferred foraging in areas of higher wave heights and higher amounts of atmospheric water than cool season adults (Table 5.4).

When comparing observed foraging locations with available foraging locations, *H. helena* during the hot season appeared to use waters with cooler sea surface temperature than were available at alternative locations, but conversely used warmer waters than were available in the cool season (Table 5.5). Likewise, in the cool season *H. helena* foraged at locations with a more easterly wind component than available at alternative locations, while during the hot season they used foraging locations with a more southerly wind component than available at alternative locations. There was no evidence that chlorophyll *a* concentration had any effect on the choice of foraging location within the cool season (95% CI -0.01-0.00, $P = 0.958$, Table 5.5) when it was relatively high everywhere, but during the hot season, when chlorophyll *a* concentrations were overall lower, the storm petrels selected foraging locations with higher chlorophyll *a* concentration than was available at alternative available locations.

Table 5.3a) Competing generalized linear mixed models (GLMMs) used to assess which environmental variables were associated with where *H. helena* foraged on a long trip from St Helena. Year and trip identification were set as nested random effects (Y/T). Individual identity (ID) was also set as an additional random effect, and season and breeding stage as fixed factors. **b)** Analysis of significance of variables in model 5. SST = sea surface temperature (C°), CHLA = Chlorophyll a Concentration (mg m⁻³).

a) Competing models

Model	Random effects	k	AICc	Delta AIC	AICcWt	Cum.Wt
(5) - SST	Y/T + ID	11	2980.54	0.00	0.39	0.39
(4) - Cloud	Y/T + ID	12	2981.88	1.33	0.20	0.86
(3) - Wind speed	Y/T + ID	13	2983.47	2.92	0.09	0.95
(2) - CHLA	Y/T + ID	14	2985.37	4.83	0.03	0.99
(1) Global ^a	Y/T + ID	15	2987.39	6.85	0.01	1.00

b) Parameter estimates of model 5

Variable	estimate	std error	Z value	P value
Current speed	-0.158	0.030	-5.176	<0.001
Sunshine	-0.101	0.028	-3.646	<0.001
Wave height	0.116	0.038	3.045	0.002
Atmospheric water	-0.122	0.039	-3.087	0.002
Sea level pressure	0.068	0.041	1.647	0.099

^a The global model contains all variables (sea surface temperature, current speed, wave height, sunshine duration, sea level pressure, cloud cover, Chlorophyll a concentration, wind speed and atmospheric water). Other models denote the term that was removed from the global model, and the resulting change in AICc. Model selection was based on AICc values.

Table 5.4. Mean values of environmental variables for foraging locations between seasons on long trips. The *P* value indicated whether the environmental parameter in the model is different from 0 and bold typeface indicates significant seasonal interaction. R^2 : proportion of variance explained by the generalised linear mixed model with a season fixed effect. *n*: number of locations from which environmental data were available.

Environmental Variable	Type	<i>n</i>	Cool season	Hot season	R^2	<i>P</i> value
			Mean $\pm$ sd	Mean $\pm$ sd		
Chlorophyll a concentration (mg m ⁻³)	Oceanographic	879	0.09 $\pm$ 0.02	0.08 $\pm$ 0.03	0.001	0.787
Current speed (m/s)	Oceanographic	966	0.07 $\pm$ 0.03	0.08 $\pm$ 0.04	0.000	0.655
Euphotic depth (m)	Oceanographic	328	103.33 $\pm$ 10.32	112.44 $\pm$ 26.30	0.000	0.745
Sea surface temperature (°C)	Oceanographic	966	23.12 $\pm$ 0.73	21.27 $\pm$ 0.39	0.215	0.001
Wave direction (degree)	Oceanographic	966	174.19 $\pm$ 25.35	148.24 $\pm$ 23.21	0.146	0.002
Wave height (m)	Oceanographic	966	2.29 $\pm$ 0.58	2.15 $\pm$ 0.39	0.017	0.618
Air temperature (°C)	Atmospheric	966	21.68 $\pm$ 1.06	20.36 $\pm$ 0.52	0.231	0.592
Atmospheric water (kg m ⁻²)	Atmospheric	966	19.61 $\pm$ 4.45	22.59 $\pm$ 3.26	0.075	0.003
Total cloud cover (0-1)	Atmospheric	966	0.55 $\pm$ 0.28	0.79 $\pm$ 0.21	0.011	0.002
Sea level pressure (kPa)	Atmospheric	966	101.87 $\pm$ 0.14	101.75 $\pm$ 0.19	0.020	0.134
Wind speed (m/s)	Atmospheric	966	6.67 $\pm$ 2.29	7.73 $\pm$ 1.30	0.167	0.001
Wind direction (degrees)	Atmospheric	966	302.10 $\pm$ 62.90	331.93 $\pm$ 10.13	0.158	0.037

Table 5.5. Mean values of environmental variables at locations used within a season for foraging and foraging locations that would have been available if birds had foraged at the same locations that birds used in the alternative season (in a different direction from the colony, see Figure 5.2). The *P* value indicated whether there was evidence of a non-zero difference of the environmental parameter between foraging and available locations in the respective seasons.

Cool Season							
Environmental Variable	Type	Mean used	Mean available	Mean difference	lcl	ucl	P
Air temperature (°C)	Atmospheric	21.68	19.93	1.76	1.63	1.88	< 0.001
Total cloud cover (0-1)	Atmospheric	0.55	0.66	-0.11	-0.15	-0.08	< 0.001
Rain (mm)	Atmospheric	0.07	0.01	0.05	0.04	0.07	0.006
Wind direction (degrees)	Atmospheric	302.10	327.45	-25.31	-32.12	-19.1	< 0.001
Wind speed (m/s)	Atmospheric	6.67	7.84	-1.17	-1.45	-0.89	< 0.001
Chlorophyll a concentration (mg m ⁻³)	Oceanographic	0.10	0.10	-0.01	-0.01	0.00	0.958
Sea surface temperature (°C)	Oceanographic	23.12	20.56	2.56	2.47	2.66	< 0.001
Wave direction (degree)	Oceanographic	174.19	149.90	24.29	21.12	27.44	< 0.001
Wave height (m)	Oceanographic	2.29	2.11	0.18	0.11	0.25	0.004
Hot Season							
Air temperature (°C)	Atmospheric	20.36	22.2	-1.85	-1.93	-1.76	< 0.001
Total cloud cover (0-1)	Atmospheric	0.79	0.54	0.24	0.22	0.27	< 0.001
Rain (mm)	Atmospheric	0.12	0.02	0.11	0.1	0.12	< 0.001
Wind direction (degrees)	Atmospheric	331.93	308.69	23.2	17.97	28.76	< 0.001
Wind speed (m/s)	Atmospheric	7.73	6.06	1.68	1.45	1.89	< 0.001
Chlorophyll a concentration (mg m ⁻³)	Oceanographic	0.09	0.07	0.02	0.02	0.03	< 0.001
Sea surface temperature (°C)	Oceanographic	21.27	23.65	-2.38	-2.45	-2.32	< 0.001
Wave direction (degree)	Oceanographic	148.24	168.77	-20.52	-23.52	-17.57	< 0.001
Wave height (m)	Oceanographic	2.15	2.11	0.05	-0.01	0.1	< 0.001

5.6. Discussion

This study provides the first description of the distribution and behaviour at sea of *H. helena* breeding at St Helena in the South Atlantic. As observed in previous studies of *Hydrobates* spp. (Bolton, 2020; Rotger *et al.*, 2020; Pascalis *et al.*, 2021; Medrano, Militão, *et al.*, 2022), *H. helena* are highly pelagic. Breeding stage strongly influenced long foraging trip characteristics; during incubation, petrels made trips that were three times longer in duration, and over two times longer in terms of distance from the colony, compared to adults rearing chicks. I also show that seasonal differences in foraging trip direction and spatial distribution are driven by differing oceanographic and atmospheric preferences of birds breeding in the hot and cool seasons, respectively.

5.6.1. Environmental factors driving genetic divergence

This study found evidence that *H. helena* optimise their foraging each season through wind direction and Chlorophyll *a* concentrations shaping their travel costs and rewards in terms of energetics. These environmental differences manifested as seasonally differing foraging directions from the colony, leading to strong spatial foraging range segregation between the seasonal populations. Environmental differences in resource availability may therefore be a driving factor behind the seasonal segregation of the *H. helena* population, which in some other populations of the *H. castro* s.l. species complex has been shown to lead to sympatric speciation through allochrony (Friesen *et al.*, 2007; Taylor and Friesen, 2017). More broadly, these results suggest that diverging at-sea distributions of seasonally segregated populations may be early drivers of sympatric speciation in seabirds (e.g., Taylor *et al.*, 2018).

Ecological overlap between non-breeding adults from the alternative breeding season is possible, but limited evidence of seasonal overlap was found at the colony (Chapter 3). The limited genetic differentiation at dRAD and mitochondrial DNA markers between the seasonal populations on St Helena (Taylor *et al.*, 2019) suggest that these populations may only be at an early stage of genetic divergence. Hence, the two seasonal breeding populations may in fact still be connected by gene flow. However, the long generation time (Storm-petrels can exceed 30 years Fransson *et al.*, (2023), renders genetic drift slow, so genetic divergence is expected to be lagging behind ecological differentiation, as e.g., suggested for Hawaiian and Galapagos petrels (*Pterodroma sandwichensis* and *Pterodroma phaeopygia*) (Welch, Yoshida and Fleischer, 2011). Hence, the segregation in foraging range between seasons could also represent changes that are too recent, or too temporally unstable, to impact the genetic structuring of the species. Future investigations

of seasonal differences in non-breeding distributions may offer further insights into opportunities for gene exchange between seasonal breeders.

5.6.2. Short trip characteristics and distribution

Some small petrel species are known to employ a dual or bimodal foraging strategy e.g., blue petrel (*Halobaena caerulea*) and thin-billed prion (*Pachyptila belcheri*) (Chaurand and Weimerskirch, 1994; Weimerskirch *et al.*, 1994), alternating between short trips to provision for a chick and long trips for maintenance of parental body condition. In contrast, the present study only identified short trips during the incubation phase. Although the limited sample size during chick rearing may have missed this dual foraging behaviour pattern during chick-rearing, my results are consistent with previous findings of other storm petrel *Hydrobates* sp. exhibiting no evidence of a dual foraging strategy (Bolton, 2020; Rotger *et al.*, 2020; Pascalis *et al.*, 2021).

The leeward distribution of short trips may be a consequence of the location of the colony at St Helena (on the leeward side of the island) or the trip duration (average 8.39hrs) limiting travel distance. The majority of short trips were identified in the 2019 cool season (Appendix 2, Table A2.2) which may be an artefact of an improved monitoring schedule or an indication of poor feeding conditions (Chaurand and Weimerskirch, 1994). Temporary egg neglect in Procellariiformes is relatively common (Boersma and Wheelwright, 1979). As an adaptive response to harsh nesting conditions and long incubation periods, many pelagic seabird eggs have evolved to be variably resistant to chilling, enabling incubating adults to temporarily neglect their egg to replenish their body reserves (Boersma, 1982; Gaston and Powell, 1989). However, egg neglect may increase the likelihood of hatching failure and chick mortality. The higher occurrence of egg neglect and thus short trips observed during the cool seasons in my study supports previous findings in Chapter 3 of lower hatching success during the cool season than in the hot season. However, given that breeding adults during the cool season experience a cooler climate than the hot season, making thermoregulation in the artificial nest chambers less challenging, one might expect hot season breeding adults to have a higher occurrence of egg neglect if indeed thermoregulation influences egg neglect. Short trips occurred predominantly during daylight hours, suggesting that daytime foraging may occur near to the colony, if adults leave the egg unattended specifically to forage. It also suggests that incubating *H. helena* may not rely entirely on long trips for self-provisioning, but given the temporal resolution of the data it was not possible to examine foraging behaviour during short trips.

5.6.3. Activity and foraging behaviour

I show that departures of adults from the colony can occur fairly uniformly across the 24-hr cycle, whereas the majority of birds arrived back to the colony at dusk. The diel distribution of foraging-type behaviour indicated that foraging was more likely to occur during the day than at night, predominantly during the early hours of the morning (Figure 5.3). Previous research has attributed daytime foraging to higher food availability and lower predation risk (Poot, 2008). However, the predation risk for petrel species at St Helena is likely to be low as there are no resident predatory bird species such as gulls or birds of prey (Rowlands *et al.*, 1998).

Breeding season was a significant predictor of foraging behaviour on long trips. Adults during the hot season were more likely to spend a higher proportion of time foraging compared to the cool season (Figure 5.3). Hot season adults also utilised areas of significantly lower productivity than available areas compared to the cool season (Table 5.5), which can negatively affect prey availability (Puerta *et al.*, 2015) and thus the need for increased foraging time. There was little evidence of differences in foraging behaviour between breeding stages and in contrast to male and female Leach's Storm-petrels (*Hydrobates leucorhous*) that have differing foraging strategies (Mauck *et al.*, 2023), little difference was observed between sexes in foraging trip characteristics during my study, suggesting equal foraging effort and exploitation of similar resources.

5.6.4. Long trip characteristics and distribution

The population of *H. helena* in this study showed a highly pelagic lifestyle, with adults on long trips travelling extended distances (up to 3285km during incubation, and 2243km during chick rearing), one of the furthest foraging distances recorded for any breeding *Hydrobates* species (Oppel *et al.*, 2018; Bolton, 2020; Rotger *et al.*, 2020; Medrano, Militão, *et al.*, 2022; Medrano, Saldahna, *et al.*, 2022; Neves *et al.*, 2023). *H. helena* showed a foraging strategy typical of many other seabird species, undertaking longer foraging trips, extending further from the colony and covering a larger area during incubation than during chick rearing, reflecting the higher energy demands of the growing chick requiring more frequent food deliveries by adults (Weimerskirch *et al.*, 2010).

Despite the two seasonal populations having similar trip characteristics (duration, max distance and total distance), trip direction and at sea distribution were significantly different. Given the temporal isolation exhibited by the seasonal populations of *H. helena* (Chapter 3), one might expect similar spatial distributions and foraging preferences as the two seasonal populations do not compete with each other. The spatial overlap between seasons was generally low, however (mean spatial overlap of UD_s = 27.9 ± 6.0) with just

a moderate BA index (0.502). These distinct season-specific patterns in the foraging behaviour and consistent between-year within-season spatial overlap suggests that adults breeding in different seasons have developed differing behaviours, rather than annual variation driving differences. This represents a high level of spatial diversity and behavioural adaptability in foraging behaviour for the species. Likewise, marked seasonal spatial segregation has been observed in other *Hydrobates* sp. (Medrano, Militão, *et al.*, 2022).

The larger marine distribution of *H. helena* during the cool season compared to the hot season suggests that cool season adults were more flexible in the areas that they foraged in, yet they spent on average less time foraging. Potential causes of this difference are either greater prey density during the cool season, or prey may have been of higher quality, therefore requiring less foraging effort.

In areas such as the relatively featureless tropical South Atlantic Ocean, where St Helena Island is located (isolated far from the nearest continental shelf/slope), seabirds often rely on oceanographic features which provide areas of higher productivity due to upwelling, such as seamounts and eddies that are within an accessible foraging range from the breeding colony. Breeding seabirds, which have to forage from a central location (the nest site) will often repeatedly utilize foraging areas where prey is consistently abundant (Hamer *et al.*, 2001; Staniland, Boyd and Reid, 2007). However, in my study, whilst *H. helena* distribution overlapped with a number of seamounts that are known to be regularly exploited by several large pelagic fish and ray species (Perry *et al.*, 2020; Beard *et al.*, 2021; Laptikhovsky *et al.*, 2021) they were not noticeably utilised for foraging, implying that environmental features may not be important drivers of prey availability and/or foraging activity in this species. However, the smaller marine distribution observed in the hot vs. cool season, together with the increased proportion of time spent foraging, supports the idea of repeated utilization of foraging areas driving their foraging strategies.

My study showed little evidence of differences in the foraging ecology between the sexes. Incubating females undertaking long trips travelled for longer durations and distances, to more distant areas than males (averaging 60km further from the colony, 197km more total distance travelled, and for 18.6 hours longer, Table 5.1). These differences were likely attributed to the higher energetic costs associated with egg production driving females to self-provision more than males (Welcker *et al.*, 2009; Hedd *et al.*, 2014; Quillfeldt *et al.*, 2014).

This study identifies the marine ranges of hot season and cool season *H. helena* populations, both of which travelled extensively beyond the MPA boundary. There are

therefore likely to be large areas of important habitat for *H. helena* outside the MPA that are currently lacking sufficient protection. The species' overall distribution was over twice as large as the MPA, however, there was large season-specific variability in coverage between the MPA and marine distribution, as well as differences between breeding stages. In particular, I found a higher proportional overlap in core area (50% UD) with the MPA boundary in the hot (74%) vs. cool (44%) season, and between chick rearing (83%) vs. incubation (58%). This highlights the importance of evidence-based advice when developing and designating MPA boundaries, which are often based on fixed distances away from the coast, or as in the case of St Helena, an existing Exclusive Economic Zone (EEZ) (St Helena Government, 2022). Coastal, colony-centred MPAs will not provide adequate protection for pelagic species such as *H. helena* which, as shown here, have large foraging ranges (Game *et al.*, 2009), and may face a range of threats at sea that require large scale approaches to mitigate effectively (Oppel *et al.*, 2018).

5.6.5. Environmental influences on foraging behaviour

This study identified a broad range of oceanographic and atmospheric features that influence the probability of foraging at specific locations whilst on a long trip. Chlorophyll *a* concentration, which is widely used as a proxy for marine productivity and thus prey availability, explained the least amount of variation in foraging probability (Table 5.3a). Instead, breeding *H. helena* were more likely to forage at locations with high wave heights, slow currents, with low levels of atmospheric water and when it was dull (low sunshine duration), however the low R^2_{marginal} value of the final model (<10% of variance explained) implies that there may be additional unidentified factors influencing foraging behaviour.

My study population also showed that seasonally contrasting features influence foraging. Breeding adults during the cool season selected foraging locations with warmer sea temperatures, slower wind speeds, lower amounts of cloud cover and atmospheric water. In contrast, hot season breeding adults foraged where the sea was cooler, in stronger wind speeds, higher levels of cloud cover and higher levels of water in the atmosphere.

Generally, to reduce the energetic costs associated with flapping flight, Procellariiform seabirds orient with crosswinds and tailwinds, to maximise flight speeds relative to the ground or sea surface (Spear and Ainley, 1997b, 1997a; Weimerskirch *et al.*, 2000). Further examination of differences between seasons in trip direction and wind speed in relation to wind and wave direction may offer more insights into foraging ecology and flight energetics. Although not examined here, wind direction is likely to play a key role in

foraging decisions, as storm petrels are particularly reliant on their olfactory senses when searching for food (Bonadonna, 2009).

My study demonstrates that seasonal populations of *H. helena* from St Helena exhibit differences in foraging distribution between their respective breeding seasons, with the hot-season population foraging primarily to the SW of the island, and the cool population foraging primarily to the SE of the island. However, I found little evidence that seasonally varying environmental conditions could explain this shift in the foraging distribution. It is possible that during the cool season when marine primary productivity is high, birds select foraging areas that maximise supportive tailwind components during their return trip, thus leading to foraging locations to the SE of the island during the cool season, whereas overall productivity during the hot season appears to be lower, forcing birds breeding at that time to select waters of relatively higher productivity and navigating a delicate trade-off between more reproductive waters and more difficult cross-wind conditions during their return flights to the colony. There may be other environmental variables not examined in this study that might explain the drivers behind the seasonally different distributions. These distributions may be ancestrally inherited preferences that have led to the seasonal segregation of the population (cause) or the seasonal populations may have evolved to prefer and forage in contrasting environmental conditions as a result of different foraging areas at sea (consequence).

5.7. Conclusions

This study offers insights into the drivers of the different foraging strategies of a seasonally segregated population, and ultimately allochronic speciation. This research will advance our understanding of allochronic speciation in seasonally segregated populations such as those examined at St Helena. Future investigation into the diet of the *H. helena* population may offer insight into prey availability and preferences between trip types, the seasonally contrasting distributions and oceanographic and atmospheric variables that together characterised foraging probability.

My study identified breeding adult distributions from one colony in *H. helena*'s range, other life history stages such as juveniles, immatures and non-breeding adults, which can represent up to 81% of all individuals in species populations (Carneiro *et al.*, 2020) should also be considered in future tracking studies, to reduce bias when assessing the species distribution at sea. Likewise, marine distributions can differ markedly between colonies at the same locality, and between populations (Awkerman *et al.*, 2014; Quillfeldt *et al.*, 2019). Therefore, tracking of *H. helena* from other breeding locations at St Helena (e.g.,

Peaked Island, Thompson Valley Island etc) as well as on Ascension Island is needed to determine whether the same applies to *H. helena* at other breeding locations.

Given the high mobility of *H. helena* and other seabird species from St Helena and Ascension Island (see Diop *et al.*, 2018, Reynolds *et al.*, 2021, Oppel *et al.*, 2015, Oppel *et al.*, 2017, Weber *et al.*, 2021) a comprehensive assessment of important marine areas, based on tracking data from multiple colonies and species, is a key conservation goal. Identification of marine Important Bird and Biodiversity Areas (marine IBAs); areas that are globally important for the conservation of bird populations (BirdLife International, 2020) and Key Biodiversity Areas (KBAs); globally significant sites for biodiversity (Handley *et al.*, 2022), in the region would be advantageous in the future. However, increased sample sizes of tracked *H. helena*, particularly during the chick rearing stage would need to be attained for comprehensive descriptions of the marine distributions of different species and seasonal populations (Beal *et al.*, 2021).

Chapter 6.

A taste for squid: Red-billed Tropicbird diet in the South Atlantic

This chapter has been accepted for publication under the same title in *Waterbirds*.

6.1 Abstract

Examining prey choice is important for understanding the drivers of survival, breeding success and other demographic changes of tropical seabirds. We analysed spontaneous regurgitations from Red-billed Tropicbird (*Phaethon aethereus*), at St Helena, South Atlantic between 2013 to 2018. Squid from four families, fish from eight families, and one octopus species were identified. Analysis of dietary composition and diversity revealed that Red-billed Tropicbirds fed predominantly on epipelagic juvenile squid, especially Neon Flying Squid (*Ommastrephes cylindraceus*). Commercially exploited fish and species commonly used as bait and/or discarded, had a low frequency of occurrence (8.8%) and by number (3.5%) in regurgitations, indicating that tropicbirds may have a low risk of mortality by fisheries bycatch. The consumption and size of squid varied among years; 2017 had significantly smaller squid which in turn were consumed in greater proportions than in the other studied years, likely driven by prey availability. Based on the analysis of regurgitations, I found that chicks were fed larger meals (by $\sim 41 \text{ g} \pm 39 \text{ g SD}$) and higher diversity of prey compared to adults, suggesting that adults favoured selecting higher quality, heavier prey as a provisioning strategy for their chicks. The high frequency of occurrence of juvenile squid, and reliance on Neon Flying Squid, suggests that future dietary monitoring of Tropicbirds can provide valuable information about juvenile cephalopod abundance and development, with relevance both to the wider ecosystem and to fisheries management.

6.2. Introduction

Seabirds are often used as bio-indicators of marine ecosystems (Rajpar *et al.*, 2018) for example to evaluate primary productivity (Velarde *et al.*, 2013) and ecosystem health (Aliakbari, Savabieasfahani and Ghasempouri, 2011). Studying seabird foraging ecology through diet composition is essential for the comparative interpretation and understanding of the relationships between seabirds as apex predators, and the marine environment (Catry *et al.*, 2009). Monitoring fluctuations in the composition and availability of prey has been used to evaluate changes in marine resources and food webs (Cherel and

Weimerskirch, 1995; Einoder, 2009), providing information, for example, on the effects of changes in climate (Montevecchi and Myers, 1997; Ito *et al.*, 2009), fish stocks (Miller and Sydeman, 2004) and contaminants affecting ocean health (Cifuentes *et al.*, 2003; Carravieri *et al.*, 2016; Seco *et al.*, 2021). In tropical oceans, where productivity is generally low and prey is generally patchily distributed, seabirds typically use foraging strategies such as feeding in multispecies flocks associated with sub surface predators (Soanes *et al.*, 2021). In contrast, seabirds in temperate or polar environments have access to food resources that show less seasonal variation and tend to forage in habitats of known enhanced productivity such as upwellings, frontal zones and shelf edges (Ashmole and Ashmole, 1967; Weimerskirch, 2007).

Tropicbirds (Order Phaethoniiformes) are long lived pelagic seabirds with long incubation and fledging periods, lasting up to 43 and 119 days, respectively (Boeken, 2016). Tropicbirds forage by surface plunging; previous studies using conventional analysis of prey remains (Le Corre *et al.*, 2003) suggest they predominantly feed on surface-dwelling flying fish (Exocoetidae) and squid (Ommastrephidae). Red-billed Tropicbirds (*Phaethon aethereus*) have a pantropical oceanic distribution, occurring in the Atlantic, Pacific and Indian Oceans (Orta, 1992; Lee and Walsh-McGehee, 2000). Unlike White-tailed Tropicbirds (*Phaethon lepturus*) that commonly forage in multi-species seabird flocks (Ainley, Spear and Boekelheide, 1986; Hyrenbach *et al.*, 2013), Red-billed Tropicbirds and Red-tailed Tropicbirds (*Phaethon rubricauda*) forage solitarily for prey, primarily at dawn and dusk (Diop *et al.*, 2018; Madden *et al.*, 2022; Madden, Boehm and Mielke, 2023) in the upper 3-10m of the water column (Sommerfeld and Hennenke, 2010; Castillo-Guerrero, Guevara-Medina and Mellink, 2011). Whilst annual differences in diet composition have been observed in Red-tailed Tropicbird (Le Corre *et al.*, 2003), few have been described in Red-billed Tropicbirds (Castillo-Guerrero, Guevara-Medina and Mellink, 2011).

Likewise, few studies of tropicbirds have compared information of the diet of adults and chicks. Indeed, when adult and chick diet has been examined, data has either been pooled together e.g., Diamond (1975); Harrison *et al.*, (1983) or used in a comparative analysis of diet composition between species from the same locality (Stonehouse, 1962; Ashmole and Ashmole, 1967; Catry *et al.*, 2009), or to quantify provisioning effort and frequency (Schaffner, 1988), inter-annual variation (Le Corre *et al.*, 2003) or environmental effects (Castillo-Guerrero, Guevara-Medina and Mellink, 2011). Understanding seabird prey requirements and dietary flexibility through different life stages is important for effective conservation and management (Cherel and Bocher, 2022)

especially in a changing climate where distribution and abundance of available prey may vary significantly over time (Reynolds *et al.*, 2019).

Assessing the threat that fisheries pose to long lived seabird species through either deletion of/competition for certain fish species or bycatch (incidental mortality) is vital for species conservation, but also to inform evidence-based fisheries management. St Helena Island holds one of the southernmost breeding sites of Red-billed Tropicbirds in the South Atlantic, representing a regionally and internationally important part of the global population (Chapter 2). The artisanal tuna fishery operating throughout the year at St Helena consists of a small inshore fishing fleet, targeting primarily Yellowfin Tuna (*Thunnus albacares*) and Skipjack (*Katsuwonus pelamis*) using pole and line and/or rod and reel. Tuna are attracted to the vessel using small pelagic fishes as bait. Trolling is also used and involves lines with artificial lures being towed behind the vessel, near to the surface at a certain speed (around ~7 knots) to attract large pelagic fish such as Wahoo (*Acanthocybium solandri*). Assessing the potential risk of this fishery for Red-billed Tropicbirds is urgently required, particularly to ensure that sustainable fisheries practices are used within the "category VI sustainable use" (St Helena Government, 2022) 200 nautical mile Marine Protected Area (MPA) around St Helena. Assessing the susceptibility of this species to threats from fisheries is also fundamental for its effective global conservation management.

The primary goal of his study was to describe the diet of Red-billed Tropicbirds at St Helena, combining conventional identification methods with molecular diagnostics, to firstly assess whether existing fisheries might pose a risk of bycatch or prey depletion based on tropicbird prey composition, and secondly to assess differences in prey composition in relation to life stage and annual variation. We hypothesised that 1) diet would consist primarily of fish and squid, as documented by observations of Red-billed Tropicbirds in the eastern Atlantic Ocean (Diop *et al.*, 2018), Gulf of California (Castillo-Guerrero, Guevara-Medina and Mellink, 2011), and Pacific Ocean (Spear, Ainley and Walker, 2007), 2) that the diet of breeding and non-breeding adults would differ in taxonomic composition due to differences in foraging strategies and the constraints imposed by central-place foraging whilst breeding, 3) that the diet of adults and chicks would differ in taxonomic composition, and 4) that there would be variation between years in dietary composition.

6.3. Methods

6.3.1. Prey sampling and identification

This study was conducted at St Helena, South Atlantic Ocean (15° 57' 57"S, 5° 42' 39"W) during colony visits carried out between 21 August and 21 December, to coincide with the peak breeding period (Chapter 2) from 2013 to 2018. Red-billed Tropicbird food samples (henceforth referred to as "regurgitations") were obtained opportunistically from adults and chicks which regurgitated spontaneously when handled. Regurgitations were processed at the Environment and Natural Resources Division laboratory of St Helena Government, St Helena. Each regurgitation was washed with water, weighed, and then prey items were separated, and items individually weighed. Red-billed Tropicbirds sometimes regurgitated many cephalopod beaks (keratinous mandibles), which accumulate in the gizzard. These accumulated prey items were separated from fresh (recently consumed/intact) prey items and processed separately. Identification of prey was made based on Smith and Heemstra (2012) for fishes, Clarke (1986) and Nesis (1987) for squid, and our own reference collection. Where identification was uncertain, prey samples were preserved and stored in alcohol (70%) until they could be sent off island for external verification by experts and/or DNA analysis.

The total length (TL, to the nearest 0.1 mm) and fresh mass (M to the nearest 1 g) of all intact fish, lower rostral length (LRL) for squid beaks, and lower hood length (LHL) for octopus beaks were measured to the nearest 0.01 mm using Vernier callipers. Regression equations given by Clarke (1986) and Xavier and Cherel (2009) for cephalopods and Smale (1993) for octopods, were used to estimate dorsal mantle length (ML) and fresh mass (M) from LRL or LHL. Where no relationships were available for a species, ML and M were extrapolated from equations for closely related species or for species with a similar morphology.

Three indices were used to describe Red-billed Tropicbird diet: percentage frequency of occurrence (%FO), average percentage abundance (%A) and percentage prey specific number (%PN) (Amundsen, Gabler and Staldvik, 1996). Species commonly encountered by local fisheries (Collins, 2016) were used to further categorise identified prey items into commercially fished species (CFS), species commonly used as bait (B) and species accidentally caught during fishing practices and discarded (D). Risk of bycatch was assessed from the cumulative percentage frequency of occurrence (%FO) and numerical abundance of each category.

6.3.2. Prey DNA isolation and amplification

A representative selection of tissue from prey items that could not be formally identified to species level from examination (15 squid) were then used to extract genomic DNA for genetic barcoding. A standard lysis/Proteinase K digestion was conducted, followed by an ammonium acetate salt and subsequent ethanol precipitation (Aljanabi and Martinez, 1997). Three separate primer pairs were used on all samples; LC01490_CephF (5'-TTTCAACAAATCATAAAGATATTGG-3') and HC02198_CephR (5'-ACTTCTGGGTGACCAAAAAATCA-3') (Braid, McBride and Bolstad, 2014) were used to amplify a 658bp region of the 5' end of the mitochondrial cytochrome *c* oxidase subunit I (CO1) gene. LCO1495N (5'-ACAAAYCATAAAGAYATTGG-3') and COI6785R1 (5'-GTAAATATATGRTGGGCTCA-3') were used to amplify the upstream region of the mitochondrial COI gene (Wakabayashi *et al.*, 2012), and a part of 16S rRNA was amplified using primer pair 16Sar (5'-CGCCTGTTTATCAAAAACAT-3') (Simon *et al.*, 1994) and 16Sb (5'-CTCCGGTTTGAACTCAGATCA-3') (Xiong and Kocher, 1991).

DNA amplification by polymerase chain reaction (PCR) was performed in 30 µl reaction volumes containing 0.8 µl Bovine Serum Albumin (BSA) (New England Biolabs, Ipswich, MA, USA), 6 µl 5x GoTaq™ Green reaction buffer (Promega, Madison, Wisconsin, USA), 2.4 µl MgCl₂ (25 mM), 2 µl dNTPs (2.5 mM each), 1.0 µl of each primer (10 µM), 0.1 µl GoTaq™ DNA polymerase (5 U/µl, Promega), 14.3 µl H₂O, and 2 µl of extracted template DNA.

The thermal cycling conditions for the Ceph and 16S primers were as follows: one minute at 94°C followed by five cycles of 40 seconds at 94°C, 40 seconds at 45°C and one minute at 72°C. Next 35 cycles of 40 seconds at 94°C, 40 seconds at 51°C, one minute at 72°C, then an extension of five minutes at 72°C. Thermal cycling parameters for LCO1495N/ COI6785R1 consisted of three minutes at 95°C, followed by 40 cycles of 45 seconds at 95°C, 45 seconds at 46°C, 1 minute 30 seconds at 72°C, then an extension of 10 minutes at 72°C. PCR products (5 µl) were electrophoresed on 2% agarose gels at 120 V for 30-40 minutes and visualised by staining with SYBR Safe® (Invitrogen, Eugene, OR, USA) and transillumination with UV light.

3 µl of PCR products showing strong bands were then mixed with 12 µl of ddH₂O for Sanger sequencing. A 15 µl subset of PCR products showing weak bands were further treated with 0.25 µl Exonuclease I (*E. coli*) (New England Biolabs), 0.5 µl Thermosensitive Alkaline Phosphatase (TSAP) and 1.25 µl MULTI-CORE™ buffer (both from PROMEGA Madison, WI, USA) to remove the oligo-nucleotide primers and surplus dNTPs. This mix was incubated for 30 minutes at 57°C, then kept for 15 minutes at 80°C for enzyme

deactivation. Next, 10 µl of the resulting PCR product were mixed with 5 µl H₂O and sent for Sanger sequencing in both directions by Eurofins (Wolverhampton, UK).

6.3.3. Taxonomic assignments of prey

Chromatograms from sequence data were checked for quality and edited using MEGA, v.7.0.21 (Kumar, Stecher and Tamura, 2016), then compared to those in the GenBank nucleotide database using the BLAST algorithm (Altschul *et al.*, 1990) (<http://blast.ncbi.nlm.nih.gov/cgi>). Assignments were made to the highest possible taxonomic level (e.g., order, family, genus, species) based on percentage of similarity. Matches of 98-100% to the best hit in BLAST, and were recorded or adjusted if the top-matching species did not occur in the south Atlantic. Sequences belonging to taxa other than the possible prey species (e.g., humans etc) were repeated and/or discarded from further analysis.

6.3.4. Statistical analyses

All statistical analyses were performed in R 3.5.1 (R Development Core Team, 2021). All general linear models (GLMs) and chi-squared tests were implemented in the *stats* package (R Core Team and contributors worldwide 2021), and all generalised additive mixed models (GAMMs) in the *gamm4* package (Wood & Scheipl, 2020) following Thomas *et al.*, (2017). Significant effects ($P < 0.05$) in final models were plotted using the *ggplot2* R package (Wickham 2016).

For the calculation of %FO, %A and %PN we excluded 27 regurgitations (23%) including 49 fresh and 6 accumulated prey items as they did not contain at least one item we could identify to species level. We were unable to examine relationships between fresh prey mass and taxon due to the high level of digestion observed in fish fresh prey items. As none of the dietary characteristics investigated varied with Red-billed Tropicbird sex (GLM, all $P > 0.10$; $n = 48$ regurgitations from males and 24 for females), data from males and females were pooled for comparisons between years, ages and breeding status. We used unpaired *t*-tests to examine differences in the fresh wet mass of regurgitations between ages (adults vs. chicks) and breeding status (breeding vs. non-breeding). A one-way analysis of variance (ANOVA) was used to assess differences in the fresh wet mass of food samples between years (2014-2018). This analysis was done on adults only, since chicks were only sampled across two years (2017 and 2018).

The numerical frequency of a given prey taxon (fish or squid) was defined as the percentage of fresh prey items of that taxon in a regurgitation. A weighted binomial general linear model (GLM; Thomas *et al.*, 2017) was then used to assess differences in diet between ages, and using adult data only we examined differences between breeding

status and among years (2013-2018). In each model, the variable of interest (year, age or breeding status) was used as an additive and interactive effect, with taxon as a categorical variable.

A GLM was used to investigate differences in the occurrence of only fish, or only squid or both fish and squid, as fresh prey in regurgitations among years. Similarly, Chi-squared tests were used to test for differences in fresh prey composition (fish, squid, or both) between ages and breeding status.

We used GAMMs to investigate whether cephalopods consumed by Red-billed Tropicbirds varied in size among years (2015-2018), between breeding status and between ages using lower rostral length (LRL) instead of mantle length (ML) to avoid extrapolation errors, and a subset of cephalopod species with a %FO >5. In all models we used a gamma distribution and log link function, with individual identity as a random effect to account for repeated measures from the same individuals. Julian day (day of the year) was treated as a smoothed fixed effect to account for seasonal variation in prey size. Year was included as a fixed factor in models of age and breeding status differences in diet, to account for annual variation in prey size between years. The significance criterion for all tests was set at < 0.05 . When applicable, data are presented as means $\pm$ standard deviation (SD).

6.4. Results

A total of 117 regurgitations were collected from chicks ($n = 23$), as well as breeding ($n = 32$) and non-breeding ($n = 62$) adult Red-billed Tropicbirds between 2013 and 2018. Regurgitations came from 81 individuals (Table 6.1) and of those individuals, 21 yielded more than one regurgitation (on different occasions).

Table 6.1. Number of regurgitations collected from Red-billed Tropicbird between 2013 to 2018.

Year	Adults		Chicks		total
	Incubating	Chick rearing	Roosting		
2013	3	6	8		17
2014	3		15		18
2015	6	2	10		18
2016	2	1	18		21
2017	1	5	7	16	29
2018		3	4	7	14
Total	15	17	62	23	117

6.4.1. Diet composition

The mean fresh wet mass, determined from 93 of 117 regurgitations was 55.32 ± 38.37 g SD (range 3-147 g). The regurgitations contained an average of 2.21 ± 1.64 (range 1-9 items) fresh prey items and 15.78 ± 28.85 (range 0-150 items) accumulated prey items ($n = 117$). A total of 259 fresh prey items were found in the regurgitations. Fresh prey consisted of squid (i.e., flesh and squid beaks with transparent parts) and fish (Figure 6.1a). Significantly more squid were observed (numerical frequency) than fish as fresh prey items in regurgitations (GLM; 73.3% vs. 26.6%, $z = 9.322$, $P < 0.001$; $n = 234$, Figure 6.1b). Squid also occurred as the only fresh prey in 50.4% of regurgitations (i.e., 59 out of 117 regurgitations), compared to 27.4% where both fish and squid occurred and 22.2% with only fish.

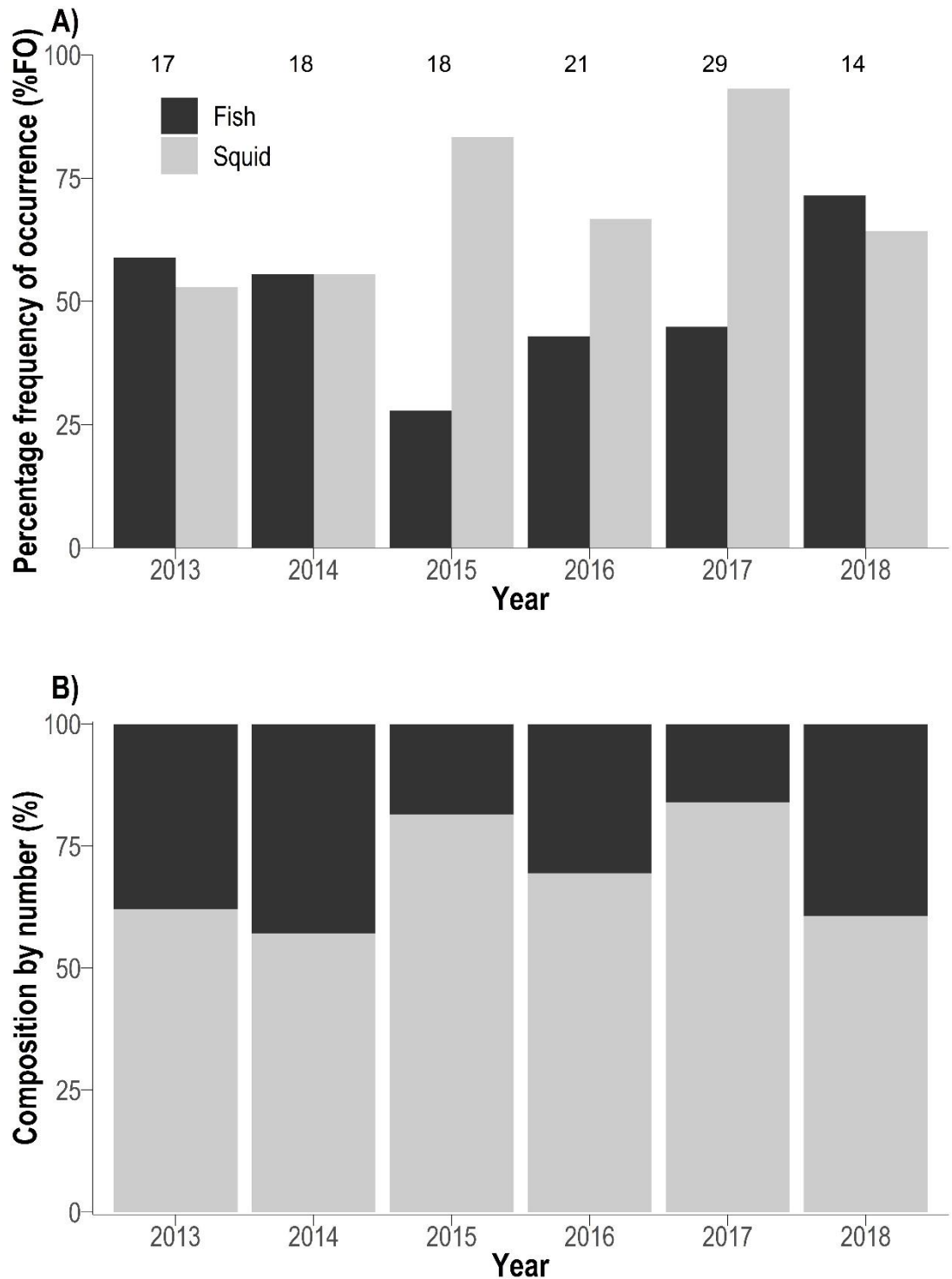


Figure 6.1. Composition of fresh regurgitations from Red-billed Tropicbirds at St Helena (adult and chicks) **a)** frequency of occurrence (%FO) and **b)** composition by number (%) per year monitored.

Eleven families, ten genera and nine species were identified from fresh prey (Table 6.2). Prey sequences were obtained for nine out of the 15 analysed regurgitated tissue samples (Supplementary Material Appendix 1). Neon Flying Squid (*Ommastrephes*

cylindraceus) had the highest overall prey occurrence (51.1% FO), while flying fishes (Exocoetidae) were the most frequently occurring fish family (22.2% FO). Three items from two regurgitations could not be assigned to either fresh or accumulated prey items; one parasitic fish isopod (unidentified Malacostraca spp.) and two parasitic copepods (*Brachiella thynni*), the latter were found in a food sample from a chick approximately four days old.

Accumulated prey items occurred in 23% of regurgitations (in 27 out of 117 regurgitations with fresh prey items), of which cephalopod beaks accounted for 97% ($n = 411$) and fish otoliths for 3% ($n = 3$) of all items. 119 cephalopod beaks from fresh prey items were collected from 52 regurgitations, resulting in a total of 276 upper and 254 lower beaks. 238 of the lower beaks were measured. Ommastrephidae was the most frequently identified prey family in the diet of Red-billed Tropicbirds, and *O. cylindraceus* the most common squid species in terms of number of lower beaks encountered (Table 6.3). The estimated ML of cephalopods for which beaks could be estimated ranged from 3.1 mm to 167.8 mm (mean = 98.9 ± 26.3 mm, $n = 238$, Figure 6.2). The species with the smallest estimated ML was Blanket Octopus (*Tremactopus violaceus*, 3.1 mm) and the largest was the Neon Flying Squid (*Ommastrephes cylindraceus*, 167.8 mm). In terms of mass, the smallest cephalopod consumed was *O. cylindraceus* with an estimated wet mass of < 1 g, whereas the largest cephalopod was Diamondback Squid (*Thysanoteuthis rhombus*) with an estimated wet mass of ~ 287 g.

Chapter 6. Red-billed Tropicbird diet

Table 6.2. Fresh prey items from breeding and non-breeding Red-billed Tropicbird regurgitations, and an indication of their occurrence in fisheries practices. Number of prey items assessed (*n*), percentage frequency of occurrence (%FO), percentage abundance (%A), percentage prey-specific number (%PN), inshore commercially fished species (CFS), inshore discards (D), bait species (B).

Class	Order	Family	Species	Totals	<i>n</i>	%FO	%A	%PN	CFS	D	B
Actinopterygii				69			26.6				
	Beloniformes			30							
		Belonidae	<i>Platybelone argalus trachura</i> *		5	4.4	1.9	55.6	-	✓	-
		Exocoetidae	Unidentified Exocoetidae		25	22.2	9.7	34.7	-	-	-
	Carangiformes			1							
		Carangidae	<i>Decapterus</i> sp.		1	1.1	0.4	100	-	✓	✓
	Perciformes			2							
		Scombridae	<i>Scomber japonicus</i> *		2	2.2	0.8	100	✓	✓	✓
	Syngnathiformes			1							
		Aulostomidae*	<i>Aulostomus strigosus</i> *		1	1.1	0.4	33.3	-	✓	-
	Tetraodontiformes			22							
		Molidae*	<i>Ranzania laevis</i> *		9	8.9	3.5	81.8	-	-	-
		Tetraodontidae	<i>Lagocephalus</i>		13	14.4	5.0	50	-	-	-
	Anguilliformes			2							
		Congridae*	Unidentified sp.		2	1.1	0.8	50	-	-	-
	Unidentified fish			11	11	6.7	4.2	33.3			
Cephalopoda				190			73.4				
	Oegopsida			190							
		Ommastrephidae	<i>Ommastrephes cylindraceus</i> *		69	51.1	26.6	52.7	-	-	-
			Unidentified Ommastrephidae		2	2.2	0.8	33.3	-	-	-
		Onychoteuthidae*	<i>Onykia carriboea</i> *		11	6.7	4.2	44.0	-	-	-
			<i>Walvisteuthis rancureli</i> *		6	4.4	2.3	50.0	-	-	-
		Thysanoteuthidae*	<i>Thysanoteuthis rhombus</i> *		1	1.1	0.4	100	-	-	-
		Unidentified squid			101	35.6	39.0	47.6			
Total					259		100				

* Indicates newly recorded prey families or species in Red-billed Tropicbird diet.

Table 6.3. Lower rostral length (LRL) for squid and lower hood length (LHL) for Octopodidae measurements (lower beaks), estimated dorsal mantle length (ML) and wet mass (g) of cephalopods identified in Red-billed Tropicbird diet ($n = 238$). % represents the proportion of each prey species in squid prey.

Prey Species	<i>n</i>	%	LRL/LHL (mm)			ML (mm)			Estimated mass (g)			
			Mean ± SD	min	Max	Mean ± SD	min	Max	Mean ± SD	min	Max	
<u>Decapoda</u>												
Octopoteuthidae*												
<i>Octopoteuthis</i> spp.	1	0.42	1.26	-	-		21.44	-	-	2.01	-	
Ommastrephidae												
<i>Ommastrephes cylindraceus</i> *	170	71.43	1.94±0.70	0.40	4.17	106.20±19.22	63.74	167.83	19.23±23.68	0.09	145.17	
<i>Hyaloteuthis pelagica</i> *	8	2.84	1.62±0.36	1.09	2.35	60.00±8.86	47.15	77.78	6.39±2.83	2.92	12.46	
Onychoteuthidae*												
<i>Walvisteuthis jeremiahi</i> *	5	2.10	1.90±0.32	1.54	2.25	87.12±19.62	65.04	108.35	13.07±6.12	6.50	20.26	
<i>Walvisteuthis rancureli</i> *	18	7.56	2.13±0.46	0.54	2.77	100.93±27.89	4.04	140.07	19.04±8.07	0.28	37.81	
<i>Onykia carriboea</i> *	28	11.76	1.87±0.42	0.70	2.65	84.97±25.89	13.80	132.75	13.24±7.84	0.61	33.10	
Thysanoteuthidae*												
<i>Thysanoteuthis rhombus</i> *	2	0.84	2.23±0.39	1.95	2.50	88.80±11.63	80.58	97.02	210.46±107.99	134.10	286.82	
<u>Octopoda</u>												
Tremoctopodidae*												
<i>Tremoctopus violaceus</i> *	5	2.10	1.54±0.47	1.00	2.18	16.79±11.89	3.09	32.81	4.47±4.42	0.76	10.98	
unknown	1	0.42										

* Indicates newly recorded prey families or species in Red-billed Tropicbird diet.

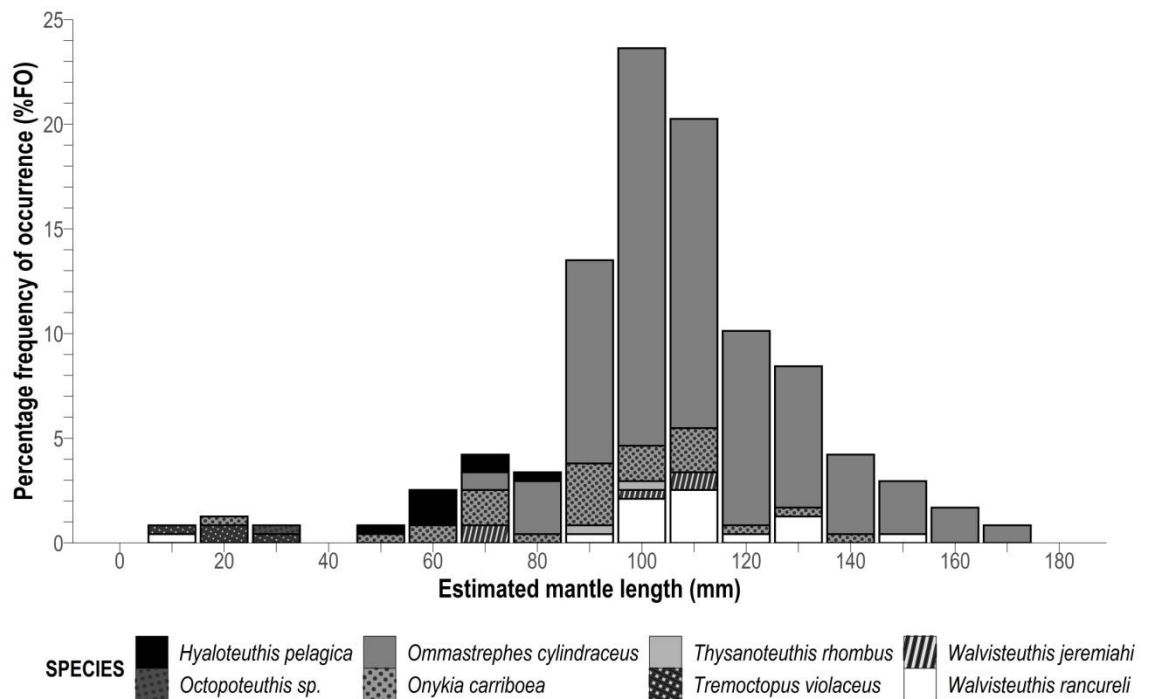


Figure 6.2. Percentage frequency of occurrence (%FO) of estimated mantle length (ML) of cephalopods consumed by Red-billed Tropicbird adults and chicks at St Helena in the South Atlantic ($n = 237$).

6.4.2. Species of fisheries interest

Altogether, species of commercial fisheries interest comprised <10% (%FO) of Red-billed Tropicbird diet. One commercially fished species; Chub Mackerel *Scomber japonicus*, was found in 2.2% of fresh diet samples (by frequency of occurrence). Two encountered taxa are commonly used as bait in fisheries: Chub Mackerel and *Decapterus* sp., collectively representing 3.3%. Four species which are occasionally discarded from commercial inshore fishing practices represented 8.8% (Club Mackerel, *Decapterus* sp., Atlantic Trumpetfish (*Aulostomus strigosus*) and Keeltail Needlefish (*Platybelone argalus trachura*) (Table 6.2).

6.4.3. Annual variation

There was no significant difference among years in the mean fresh wet mass of regurgitations (ANOVA, $F = 1.371$, d.f. = 4, $P = 0.253$; $n = 71$), or evidence of differences among years in the consumption (numerical frequency) of fresh prey per regurgitation (GLM; $z = -1.584$, $P = 0.113$; $n = 188$). However, there were significant differences in the proportion of squid among years compared to fish (GLM; year:taxon: $z = 2.017$, $P = 0.043$;

$n = 188$), with 2017 regurgitations having a considerably higher proportion of squid (mean proportion of squid: 73.1%) than those in 2013 (mean: 46.1%). The number of regurgitations containing only fish as fresh prey differed significantly from regurgitations containing both fish and squid ($t = 2.435$, $P = 0.031$; $n = 18$), and the strength of these differences varied significantly between years (fish only: years: $t = -2.435$, $P = 0.031$; $n = 18$). After accounting for variation between prey species and across Julian Days, cephalopods in Red-billed Tropicbird diet were significantly smaller in size during 2017 and 2018 than in 2015 (2017: -0.255 ± 0.094 , $t = -2.702$, $P = 0.008$, 2018: -0.456 ± 0.126 , $t = -3.623$, $P < 0.001$; $n = 198$, reference year = 2015, model $R^2 = 0.196$, Figure 6.3).

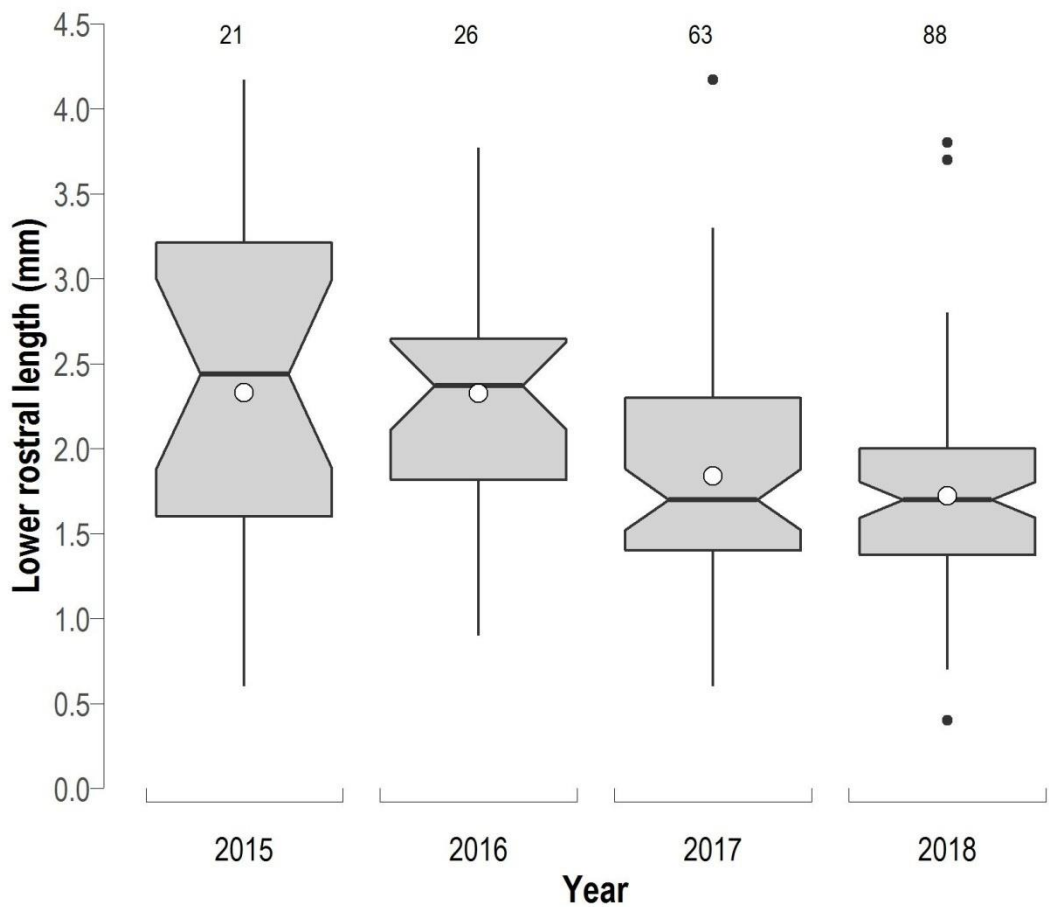


Figure 6.3. Relationship between lower rostral length (LRL) (mm) of consumed squid *Ommastrephes cylindraceus* and *Onykia cariboea* between 2015-2018 by Red-billed Tropicbird adults and chicks. Tropicbirds in 2015 consumed squid of significantly larger beak size than 2017 and 2018. The boxes show the 25th and 75th percentile, notches the median, and whiskers the maximum value excluding outliers (black dots). n : number of measured lower beaks is indicated at the top. White dots represent the mean value for each year.

6.4.4. Breeding and non-breeding adult diet

Breeding adult regurgitations had a heavier wet mass than non-breeding adults (mean $\pm$ SD for breeding: 63.07 ± 41.12 g, mean for non-breeding adults: 38.82 ± 27.66 g; unpaired t -test, $t = 2.429$, $P = 0.022$, $n = 71$). There was little evidence of differences in the occurrence of only fish, squid or both as fresh prey ($X^2_2 = 3.071$, $P = 0.215$, $n = 94$), or differences in overall consumption (numerical frequency) of fresh prey items (GLM; $\beta = -0.408 \pm 0.235$, $z = -1.738$, $P = 0.082$, $n = 188$) between breeding and non-breeding adults. However, non-breeding adults consumed more squid (numerical frequency) as fresh prey items than breeding adults did (mean proportion of squid per non-breeding adult regurgitation: 66.9% vs. breeding adult: 57.3%, GLM; $z = 2.159$, $P = 0.031$, $n = 188$). After accounting for differences within seasons (Julian Day), between years and prey species, non-breeding adults consumed only marginally smaller squid than breeding adults ($\beta = -0.075 \pm 0.084$, $t = -0.888$, $P = 0.377$, $n = 84$, $R^2 = 0.239$, Figure 6.4A).

6.4.5. Adult and chick diet

Adult regurgitations were on average 41g lighter than that of chicks (mean for adults: 45.65 ± 38.19 g, mean for chicks: 86.54 ± 37.35 g; unpaired t -test, $t = -4.645$, d.f. = 32.56, $P < 0.001$; $n = 93$). The diet of adults was considerably less diverse than that of chicks; adult regurgitations consisted predominantly of only squid as fresh prey items (54%), whereas chick regurgitations were more likely to contain both fish and squid (61%, $\chi^2 = 17.265$, d.f. = 2, $P < 0.001$; $n = 117$). We found no evidence of differences in overall consumption (numerical frequency) of fresh prey between chicks and adults (GLM; $z = -1.712$, $P = 0.087$; $n = 234$); however, chicks had a higher consumption of squid as fresh prey in regurgitations than adults (GLM, mean proportion of squid per regurgitation 74.9% vs. 63.6%, $z = 2.182$, $P = 0.029$; $n = 234$). After accounting for variation within a breeding season (Julian Day), variation between years, and prey species, chicks consumed only marginally, and not significantly smaller squid than adults ($\beta -0.058 \pm 0.081$, $R^2 = 0.193$, $t = -0.720$, $P = 0.472$; $n = 198$, Figure 6.4B).

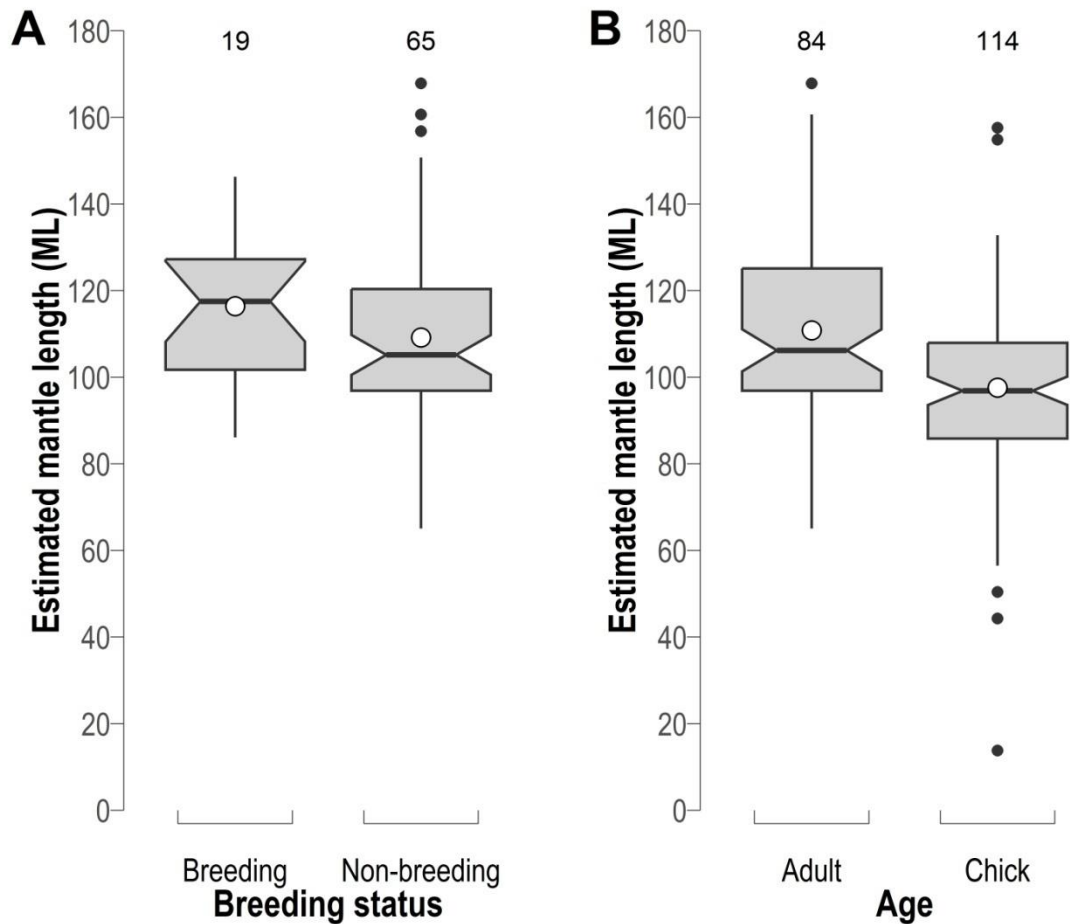


Figure 6.4. Estimated mantle length of Neon Flying Squid (*Ommastrephes cylindraceus*) and Tropical Clubhook squid (*Onykia carriboea*) consumed by A) breeding versus non-breeding adults and B) adult versus chick Red-billed Tropicbirds, respectively. The boxes show the 25th and 75th percentiles, notches the median, and whiskers the maximum value excluding outliers (black dots). *n*: number of measured lower beaks is indicated at the top; white dots: mean value.

6.5. Discussion

This is the first detailed study of Tropicbird diet in the South Atlantic, enabling us to assess the susceptibility of Red-billed Tropicbirds to fisheries-related threats. We found that the diet consisted primarily of squid, containing only small proportions (< 10%) of species that are commercially exploited in local fisheries. This indicates that Red-billed Tropicbirds on St Helena are currently unlikely to be strongly affected by the current existing local fisheries. However, squid fisheries operating in international waters, which tropicbirds frequently use for foraging (Diop *et al.*, 2018), often target the same squid species and may pose a bycatch risk or reduce the squid available for foraging tropicbirds. A recent study of Sooty Terns (*Onychoprion fuscatus*) on nearby Ascension Island

suggested depletion of fish stocks by commercial fisheries may have driven this seabird to shift its diet from fish to energetically lesser valuable squid, which correlated with declines of the breeding population (Reynolds *et al.*, 2019). It remains unclear whether Red-billed Tropicbirds on St Helena inherently prefer squid as a prey item, or whether this contemporary pattern might reflect recent changes in prey availability due to fisheries or climate change.

6.5.1. Dietary composition

Diet consisted predominantly of squid, accounting for 73.4% of fresh prey items and fish (26.6%), in contrast to Red-billed Tropicbirds in the North Atlantic which fed exclusively on fish (Diop *et al.*, 2018; Madden *et al.*, 2022). Our study found both a high occurrence (%FO) and numerical abundance of squid in the diet at St Helena, which is rare not only for Red-billed Tropicbirds, but for tropicbirds in general. In one of the two years during which Red-billed Tropicbird diet was observed using regurgitations in Farallon de San Ignacio, Mexico, cephalopods had a higher occurrence than fish (Castillo-Guerrero, Guevara-Medina and Mellink, 2011), but in all other known Red-billed Tropicbird diet studies which examined regurgitations, fish had a higher abundance and/or occurrence than squid (Diop *et al.*, 2018; Llamas, 2019; Madden *et al.*, 2022; Madden, Boehm and Mielke, 2023).

Red-tailed Tropicbird regurgitations in the eastern Pacific and at Europa Island, Indian Ocean showed an overall lower occurrence of squid but still a higher abundance (%number) of squid than fish (Le Corre *et al.*, 2003; Spear, Ainley and Walker, 2007). On Christmas Island (Indian Ocean), Red-tailed Tropicbirds showed a higher occurrence of squid than fish (Ashmole and Ashmole, 1967) in contrast to Aldabra Atoll (Indian Ocean) where the opposite was observed (smaller abundance and occurrence of squid than fish) (Diamond, 1975). Similar findings apply to diet studies of White-tailed Tropicbirds: all but one study, at Aldabra Atoll, Indian Ocean (Diamond, 1975), showed either higher occurrence and/or abundance of fish over squid (Schaffner, 1988; Ramos and Pacheco, 2003; Catry *et al.*, 2009). These differences in diet between locations from examining regurgitations are likely to be influenced by prey availability (Reynolds *et al.*, 2019), the geographical position of the colony in relation to the proximity to one or more oceanic fronts, species foraging preferences on continental shelves or oceanic waters or a combination, as seen in albatross species (Xavier, Croxall and Reid, 2003).

We recorded for the first time four families of cephalopods in the diet of Red-billed Tropicbirds, including eight genera and seven species not previously documented in the diet. Three genera of fish including two families and four species were recorded in the diet

for the first time. All species of squid recorded in the present study were new in the diet of Red-billed Tropicbirds in the South Atlantic. Although the Tropical Clubhook Squid (*Onykia carriboea*) was recorded in the diet of Fairy Terns (*Gygis alba*) as early as 1965 at St Helena (Bolstad, 2008), it has not been recorded to date in the diet of any other seabird species at St Helena.

Despite evidence of fish not playing a major role in the dietary composition, and the high level of digestion limiting identification of many fish to species level (~56%), our study demonstrates that Red-billed Tropicbird's prey on both coastal/neritic (e.g., needlefishes Belonidae) and oceanic fish (e.g., molas Molidae). Given the small number of other prey types that were included occasionally in the diet of some individuals, and all LRL were on average < 4 mm, indicating that ingested squid were epipelagic juveniles (Zuyev *et al.*, 2002), we consider it likely that the population of Red-billed Tropicbirds at St Helena specialises in foraging on juvenile Neon Flying Squid (*O. cylindraceus*).

Slender Sunfish (*Ranzania laevis*) that were present in regurgitations are known to feed predominantly on squid of the family Ommastrephidae (Nyegaard, Loneragan and Santos, 2017), it is therefore possible some accumulated cephalopod prey found in the Red-billed Tropicbird diet could have accrued through a secondary predator such as Slender Sunfish. Likewise, the detected copepods and isopod taxa could have been ingested by prey, attached to prey, or directly consumed by Red-billed Tropicbirds. Given the size of the parasitic isopods (< 1cm) it seems unlikely that the latter occurred. Ashmole and Ashmole (1967) also noted parasitic copepods and isopods in the diet of Red-tailed Tropicbirds in the Pacific Ocean, but considered them to be accidental prey, given the small number observed. It is nevertheless feasible that adult tropicbirds purposely forage for copepods to feed to small, young chicks.

Excluding the copepods and isopod that could not be defined as intentional or accidental prey, we found no additional evidence of crustaceans in Red-billed Tropicbird diet, although Penrose 1879 postulated that crabs formed a staple of tropicbird diets on nearby Ascension Island, and crabs have been recorded in small quantities in Red-billed Tropicbird regurgitations at the Gulf of California (Castillo-Guerrero, Guevara-Medina and Mellink, 2011). Similarly at Cabo Verde small quantities of crab as well as DNA from a crustacean and mollusc were found in the regurgitations of Red-billed Tropicbirds (Llamas, 2019; Carreiro *et al.*, 2023) and small quantities of shrimp have also been found in Red-tailed Tropicbird regurgitations in Hawaii (Harrison, Hida and Seki, 1983). This likely reflects regional availability instead of prey preference, given the low energetic value of such small prey items.

The current understanding of prey behaviour, and vertical distribution of oceanic squid is very limited (Boyle and Rodhouse, 2005). Squid are known to rise to the surface during the night to feed then descend to the ocean depths, 200-1000m in daytime (Zuyev *et al.*, 2002). Given that the maximum recorded diving depth of Red-billed Tropicbirds is relatively shallow (25.6 m; Sommerfeld and Hennicke 2010) one might expect foraging to occur more frequently at night when squid are closer to the surface during their vertical migration; however, the timing of foraging behaviour has yet to be examined at this locality. Red-billed Tropicbird populations in the Caribbean and Senegal tend to be inactive and rest at night, with a foraging peak in the early hours after sunrise (Diop *et al.*, 2018; Madden *et al.*, 2022; Madden, Boehm and Mielke, 2023), but this may be explained by their diet being exclusively composed of fish. Similarly, Red-billed Tropicbirds at Cabo Verde and Mexican colonies were found to dive to much shallower depths (< 3m; Castillo-Guerrero *et al.*, (2011); Saldanha *et al.*, (2023)), which may also explain their preference for fish over squid. Prey can also be made available at the upper layers of the ocean through the action of other foraging animals, e.g., tuna and dolphins, which herd prey to the surface. Tropicbirds are thought to often forage in association with sub-surface feeding predators (Ashmole and Ashmole, 1967; Ballance and Pitman, 1999; Spear, Ainley and Walker, 2007) such as tuna, which have shown a high consumption of epi- and mesopelagic prey (Perrin *et al.*, 1973). Examining the spatio-temporal foraging patterns and inter-specific interactions of the St Helena Red-billed Tropicbird population would offer additional insights into their foraging ecology. The use of additional taxonomic identification techniques such DNA metabarcoding of regurgitations or faecal samples as well as Stable Isotope Analysis could also provide further insight into predator prey trophic interactions (Carreiro *et al.*, 2023; Piña-Ortiz *et al.*, 2024).

6.5.2. Susceptibility to bycatch

The fish *S. japonicus* was the only locally commercially fished species of high global commercial value (Sumaila *et al.*, 2007) found in the Red-billed Tropicbird diet samples. *Scomber japonicus*, along with other species commonly used as bait are predominantly caught before dawn within 30 nautical miles of the coastline (Laptikhovsky *et al.*, 2020) when Red-billed Tropicbirds may forage (Diop *et al.*, 2018; Madden *et al.*, 2022; Madden, Boehm and Mielke, 2023). However, given that their foraging range from St Helena extends considerably outside the Marine Protected Area (MPA) (Diop *et al.*, 2018), the risk that local commercial fisheries pose to Red-billed Tropicbirds at St Helena is probably low.

Another component of tropicbird diet around St Helena is Roughear scad (Carangidae; *Decapterus tabl*), which is found in small numbers in tropicbird regurgitations (A. Beard

pers. obs.). In contrast Carangidae (*Decapterus* sp.) account for over 70% of bait used in commercial tuna fisheries around St Helena (Laptikhovsky *et al.*, 2020). The low incidence of commonly used bait fish (Carangidae and Scombridae) and species commonly discarded (Table 6.2) implies that Red-billed Tropicbirds are not dependent on fisheries for food, unlike other seabird species, for example Northern Gannets *Morus bassanus* (Patrick *et al.*, 2015). These results agree with findings by Diop *et al.*, (2018), who concluded that Red-billed Tropicbird breeding at Senegal may partly feed on discards but are not reliant on them. Overall, neither the risk of bycatch nor the risk of prey competition or depletion appear to currently affect tropicbirds at St Helena.

6.5.3. Annual variation

The observed differences in diet among years in our study may have been driven by annual differences in the availability of prey species. Squid were the predominant prey caught by Red-billed Tropicbirds; despite considerable variability in availability as the number and size of squid per regurgitation varied among years. There were no observed differences in the occurrence of only squid in regurgitations or occurrence between years compared to regurgitations containing only fish or both fish and squid. In the South Atlantic oceanic environment with patchy and annually varying food availability, squid may represent a more predictable and thus predominant prey compared to pelagic fish. In the Pacific Ocean, it is well understood that inter-annual variability in oceanographic conditions caused by El Niño Southern Oscillation (ENSO) has dramatic effects on entire seabird assemblages (Spear, Ainley and Walker, 2007; Pistorius *et al.*, 2023) and also affects Red-billed Tropicbird foraging behaviour and diet (Castillo-Guerrero, Guevara-Medina and Mellink, 2011). In the South Atlantic, in contrast fluctuations in the Angola Benguela upwelling system and its influence of prey availability are less understood. Although oceanographic fluctuations are not directly and quantitatively examined in my study, I note that 2015 coincided with a moderate cooling event along the Angolan-Namibian coastline (Imbol Kougue, 2018) and a significant increase in the occurrence and number of squid found in Red-billed Tropicbird regurgitations (Figure 6.1a, b). There was also among-year variability in frequencies of regurgitations containing both fish and squid prey compared with those just containing fish, suggesting fish were caught opportunistically. The degree of digestion of fish prey meant that reliable estimation of length and mass was not possible. However, fish could be larger in size and mass compared to squid, which would reduce a tropicbird's limited payload capacity to carry multiple prey items such as both fish and squid. During the 2015 Angola Benguela cooling event, adult Red-billed Tropicbirds at St Helenian showed significantly lower body condition than in other years 2013-2017 (Chapter 4), suggesting that environmental fluctuations may have impacted both prey and predators in this little-studied upwelling

system. *H. helena* showed lower breeding success in the 2017 hot season than in other seasons 2014-2019 (Chapter 3). These observations suggest possibly widespread effects by environmental fluctuations (e.g., the Angola Benguela current) on tropical Atlantic seabirds, however, more work is required to clearly link seabird population demography to these climatological features. Regardless our findings highlight the importance of multiyear studies to identify drivers of variation in diet composition.

6.5.4. Breeding vs. non-breeding adult diet

There were few differences observed in the diet between breeding and non-breeding adults. Although regurgitations were generally lighter in mass and contained a higher proportion of squid as fresh prey in non-breeding adults compared to breeding adults, there was little evidence of differences in the occurrence or frequency of fresh prey, or the size of squid consumed. This is surprising given that breeding adults are often constrained to forage within an accessible distance to the breeding colony, whereas non-breeders can forage for longer over larger distances, and therefore likely exploit different areas at sea (Weimerskirch, 2007; Buckingham *et al.*, 2023). Increased sample sizes and ideally matched tracking data may be required to better understand any niche segregations among breeding and non-breeding Tropicbirds around St Helena.

6.5.5. Adult versus chick diet

This is the first study using a traditional approach to compare Red-billed Tropicbird adult and chick diets, however Piña-Ortiz *et al.*, (2024) compared adult and chick diets using stable isotopes. Diets of adults were considerably less diverse than those of chicks. Adult regurgitations consisted predominantly of only squid, whereas chicks were more likely to contain both fish and squid. This is consistent with findings by Piña-Ortiz *et al.*, (2024) where higher stable isotopic ratios were observed for chicks than adults, suggesting that adults select higher quality prey for their chicks compared to what they consume themselves. This is a common strategy in many bird species during chick rearing; for example among crested terns (*Sterna bergii*) (McLeay *et al.*, 2009). As a chick grows there is a high energy demand, and energy-rich prey species, which have a high protein or lipid content, are often preferentially collected for delivery to young, compared to prey ingested by parents (Ojowski *et al.*, 2001). Squid are considered to have a lower calorific content due to lower contents of lipids than fish (Croxall and Prince, 1982; Zuyev *et al.*, 2002).

As expected, Red-billed Tropicbird chicks consumed larger quantities (proportion per regurgitation) of squid than adults, and slightly (although not significantly) smaller sized squid as fresh prey than adults. This may be because chicks are often constrained by

their physical capacity; smaller squid would be easier to ingest, and as chicks grow in size, so does their ability to ingest larger volumes in one feed (Schaffner, 1988). Our results suggest that Red-billed Tropicbirds at St Helena select higher quality, heavier prey for their chicks over quantity as a provisioning strategy. However, all observed differences must be interpreted cautiously, as it is possible that during the return flight from foraging areas, adult prey had been digested for a longer period than meals delivered to chicks. Similarly, it is unclear whether regurgitations from adults rearing chicks were intended for themselves or for the chick. However, the limited dietary differences observed between breeding versus non-breeding adults suggests minimal influence on the differences in adult versus chick diet. This study did not allow a comparison of the differences in prey species between adults and chicks or between different breeding stages (non-breeding, incubation and chick rearing) due to the small sample size. It would be advantageous to examine this further in the future.

6.5.6. Management implications

Both trolling and pole and line are highly selective fishing methods (Santiago *et al.*, 2016), with pole and line fishery considered to have a low associated bycatch risk for seabirds relative to other tuna fishing methods (e.g., purse seine; Miller *et al.*, 2017). Given the low incidence of commercial, bait and discarded fish species identified in the diet of Red-billed Tropicbirds, totalling 3.5% of fresh prey (Table 6.2), the fact that current fisheries management prohibits the use of less selective fishing methods (e.g., purse seine, bottom trawls, gill and tangle nets and longlining) and that illegal, unreported and unregulated fishing within the MPA is thought to be rare (St Helena Government, 2022), we consider the threat posed by current commercial fishing practices pose on Red-billed Tropicbirds within the St Helena MPA, to be low.

The Ommastrephidae family was identified as the predominant cephalopod family in Red-billed Tropicbird diet, similar to White-tailed Tropicbirds in Puerto Rico (Schaffner, 1988). Ommastrephidae are the most important commercial group of cephalopods globally, representing almost 50% of the total fished cephalopod biomass (FAO, 2019). Despite squid not currently being a target of local commercial fisheries (St Helena Government, 2022), Red-billed Tropicbirds are known to forage extensively outside of the 200 nautical mile MPA (Diop *et al.*, 2018), where commercial cephalopod fisheries occur. Future changes in fisheries practices could therefore have important implications for sustainable management of resources and potential change in susceptibility of tropicbird populations to bycatch mortality.

The large component of juvenile squid in the diet of Red-billed Tropicbirds has two important management and monitoring implications: firstly, Red-billed Tropicbirds are a suitable sentinel species to monitor for future changes in juvenile squid abundance and fisheries practices. This is particularly important, given recent work suggesting that some squid fisheries have increased by 68% in 2017-2020 while squid fisheries globally are largely unregulated (Seto *et al.*, 2023). Secondly, Tropicbird population monitoring can yield important insights into biotic effects of climate changes in tropical marine ecosystems (Le Corre *et al.*, 2003; Castillo-Guerrero *et al.*, 2011), particularly on changes in prey distribution and abundance (Diamond and Devlin, 2003).

Chapter 7.

General Discussion

7.1. Overview

The research presented in this thesis has enhanced our understanding of many aspects of the breeding and foraging ecology of two seabird species that are challenging to study. This thesis has provided important data on breeding success and productivity of the two study species (Chapters 2 and 3), both of which exhibited significant variation between years, identifying and discussing potential causes, contributing to increased local and international awareness of the species population. This thesis also illustrates the value of using artificial nest chambers (ANCs) as a monitoring tool for cavity and burrow-nesting seabird species (Chapter 3). The interactions between body condition regulation and key life history traits such as breeding regime and reproductive success examined in Chapter 4 highlighted a previously unidentified flexible sex-specific incubation routine in Red-billed Tropicbirds. Evidence was also found for spatial differences in chick growth rates in the Atlantic, significantly extending our knowledge on Red-billed Tropicbird ecology. GPS tracking technology (Chapter 5) provided information on the differing at-sea distribution and foraging behaviour between seasons of *H. helena*, providing new insights into potential drivers of speciation through allochrony. Evidence was found of a specialised diet for the Red-billed Tropicbirds at St Helena (Chapter 6), underlining the need for investigations within and between colonies in a species range to fully understand predator-prey relationships and foraging preferences.

7.2. Summary of key findings

The results in Chapter 2 quantify and contextualise the significance of the Red-billed Tropicbird population at St Helena within the South Atlantic region and within the global context of the species' range. These findings highlight the importance of appropriate conservation and management and the urgency for action, given the alarmingly low productivity observed comparatively to other populations examined. Use of cavities and nest site choice were driven by a variety of characteristics, providing insights behind the complex environmental preferences during the breeding season. Through examination of Red-billed Tropicbird breeding periodicity and phenology I identified additional influences on the breeding regime, significantly extending our knowledge on several neglected aspects of the species' breeding ecology and life history traits.

The use of ANC's for research and monitoring of cavity nesting seabirds, as described in Chapter 3, assessed their effectiveness as a conservation technique at a population level. Evidence provided in this thesis supports the usefulness of ANC's as a conservation tool, especially for species such as storm-petrels that are relatively small, nocturnal and cavity nesting. This chapter also revealed that careful consideration needs to be given to the construction materials used and installation location for any future ANC installations, to achieve high occupancy and uptake for breeding.

Given that Red-billed Tropicbirds are considered sexually monomorphic (Nunes *et al.*, 2013), the finding of flexible and sex-specific incubation routines (Chapter 4) was unexpected: males undertook longer and more frequent incubation shifts than females. I also identified between-year differences in body condition of adults, and spatial variation between two Atlantic breeding sites in the growth rates of chicks. This highlights that flexibility and adaptability in body condition regulation are likely important for threatened seabird populations, allowing them to optimise resources in an era of climate change and other anthropogenic changes to marine environments (Aebischer, Coulson and Colebrook, 1990; Watanuki *et al.*, 2009) which influence prey availability.

South Atlantic Storm-petrels (*H. helena*) at St Helena showed a pelagic at-sea breeding distribution (Chapter 5). Examination of each seasonal population highlighted marked differences in trip direction, resulting in differing marine distributions and foraging behaviour: hot season breeding adults travelled in a southwest direction, selected a smaller area but spent more time on average actively foraging than cool season breeding adults (which foraged to the southeast of St Helena). The environmental variables examined offered little evidence of the drivers in these identified seasonal differences. Whether these observed differences in foraging areas at sea were a cause or consequence of differing phenology remains unknown. Nevertheless, this research has significantly advanced our understanding of the foraging ecology of this newly designated species, within the framework of existing knowledge on other seasonally segregated *Hydrobates* species globally and their various positions along the process of allochronic speciation and the relative progression of foraging range versus genetic differentiation between the two seasonal populations (Friesen, Burg and McCoy, 2007; Taylor *et al.*, 2019). The finding of adults during the incubation period occasionally leaving the nest unattended and conducting short foraging trips was not in fact unusual for petrel species (Weimerskirch *et al.*, 1994) or indeed Procellariiformes in general (Boersma and Wheelwright, 1979; Gaston and Powell, 1989; Ronconi and Hipfner, 2009).

This research is one of few multi-year studies comprehensively examining tropicbird diet (Chapter 6). My findings indicate that Red-billed Tropicbirds at St Helena have a specialised diet, primarily consuming epipelagic juvenile squid with a particular reliance on Neon Flying Squid (*Ommastrephes cylindraceus*). A cephalopod-dominated diet is unusual for tropicbird species and indeed has only been reported once in other Red-billed Tropicbird populations, where fish are usually the primary prey. These contrasting prey preferences highlight the limited research on diet within the tropicbird family and the importance of examining diet between different localities within a species range. This essential information is needed to understand their basic foraging ecology and formulate appropriate species conservation and management strategies.

7.3. Conservation management implications and recommendations

7.3.1. Direct recommendations to support seabird nest success at St Helena

The relatively quick uptake in occupancy and use for breeding in ANCs identified in Chapter 3 suggested that availability of suitable breeding habitat may be a limiting factor for the *H. helena* population at St Helena. Thus, maintaining existing and/or provisioning of additional ANCs at other known breeding colonies will increase the availability of nest sites at a local scale. Mitigating the risk of disturbance from Brown Noddy chicks during the hot season on the offshore islets where both species are known to co-exist through, for example, provision of natural stone shelters, would also be advantageous in the future to reduce inter-specific competition and increase chick survival for *H. helena*. Such measures seem especially warranted, given the potential recognition of the south Atlantic breeding population as a distinct species.

Predation of seabirds at mainland nesting sites on St Helena has historically been a major threat to many seabird species, particularly petrels (Ashmole, Ashmole and Bourne, 1999; Beard, 2016), and is likely a limiting factor to the (re-)establishment of *H. helena* at ST Helena mainland sites. Predation was also identified as the predominant cause of chick failure in Red-billed Tropicbirds at mainland sites during my study (Chapter 2). Large scale eradication of mammalian predators has become an increasingly financially and logistically feasible option for addressing the impacts of invasive species on small island communities. Feral cat eradications have been successfully completed on many islands in New Zealand e.g., on Campbell Island and Little Barrier Island (Veitch, 2001). Other South Atlantic UKOTs where feral cats were successfully eradicated include Tristan da Cunha in 1974 and Ascension Island in 2004 (Hughes, Martin and Reynolds, 2008; Ratcliffe *et al.*, 2010). However, at St Helena, due to its size and rugged terrain, predator

control and exclusion at selected locations are thought to be a more realistic options (Hilton and Cuthbert, 2010). Improved legislation with sustained, consistent compliance with existing regulations to control free-roaming cats and dogs, in conjunction with an education awareness programme to inform pet owners, would help mitigate the threat of cats and dogs, particularly for colonies near residential areas such as Jamestown and Half Tree Hollow.

7.3.2. Future conservation and management recommendations

To ensure that offshore islets around St Helena remain predator free and thus protecting existing seabird populations using them, my research supports the development of an integrated bio-security, predator control and monitoring programme, potentially together with existing fisheries and tour operator licensing and enforcement policies and practices. Reinvestment of licensing income to look, respond and protect against bio-security threats is one strategy commonly used to create positive outcomes. This can be done through either collaboration or partnership agreements between government bodies and NGO organisations e.g., UK Environment Agencies and the Angling Trust (Environment Agency, 2023), or through set up of funding incentives to carry out surveillance and response programs e.g., Queensland Government, Australia (Queensland Government, 2022).

Future changes in fisheries practices in the South Atlantic have important implications for sustainable management of resources and potential change in susceptibility of populations to bycatch, especially for species with specialised diets such as Red-billed Tropicbirds at St Helena (Chapter 6). Despite my research indicating that the current bycatch risk was likely low for Red-billed Tropicbirds at St Helena, this situation might change if, in the future, commercial cephalopod fisheries develop and/or current practices change.

Given that the distribution of *H. helena* (Chapter 6) covered only ~35% of the area within the protected waters of the MPA, and other seabird species observed at St Helena exhibited similar highly pelagic distributions (see Diop *et al.*, (2018), Oppel *et al.*, (2015), and Oppel *et al.*, (2018)), careful reconsideration should be given to the effectiveness of the current MPA boundary in protecting these seabird species. Revision of all seabird tracking data from St Helena to quantify MPA use may be necessary to inform key stakeholders in the revision of MPA boundaries, and the development of protection measures within the MPA.

7.4. Further research

7.4.1. Climate change

Anthropogenic induced global warming has caused widespread and rapid changes in abiotic and biotic conditions in every region across the globe (IPCC, 2023). Altogether these climate changes pose a major threat to species and ecosystems (Sekercioglu, Primack and Wormworth, 2012; Hobbs *et al.*, 2021). Understanding how animal populations respond to these changes, such as more frequent extreme weather events (Frederiksen *et al.*, 2008; Hennicke and Flachsbarth, 2009), is a crucial step towards an understanding of how climate change will affect different species and is essential knowledge for development of appropriate conservation and management strategies.

In the Pacific Ocean, the impacts of El Niño Southern Oscillation (ENSO) events on seabirds key life history traits, such as longevity and reproductive success (Surman and Nicholson, 2009; Surman, W. Nicholson and Santora, 2012; Ancona and Drummond, 2013) are better understood than the influence of the Angola-Benguela upwelling system and the South Equatorial Current on seabirds in the South Atlantic (Chapter 4). Multi-year studies examining the impact of climate change on the Angola Benguela upwelling cycle and its knock-on effect in seabirds in the South Atlantic, may enable identification of conservation actions that could reduce these impacts but also enable prediction of future changes in other marine species and ecosystems. This would follow efforts for the North-East Atlantic where seabird sensitivity and adaptive capacity to climate change have been assessed (Häkkinen *et al.*, 2023), as a resource to help address each identified climate change related threat. A quantitative climate change vulnerability assessment should be completed for seabirds in the South Atlantic, to identify conservation actions aiming to reduce seabird species' vulnerability to climate change.

The impacts of climate change on marine species and their trophic relationships are still poorly understood (Harrison and Seki, 1987; Post *et al.*, 2009; Häkkinen *et al.*, 2023). Quantifying prey in seabird diet is important for understanding habitat selection and predicting how changes to marine resources impact pelagic birds. The threat these changes pose is higher for species that have highly specialised diets such as Red-billed Tropicbirds at St Helena (Chapter 6). Recent development of non-invasive molecular techniques such as DNA metabarcoding of faecal or regurgitation samples is now a reliable and feasible method to characterise diet through identification of prey items (Deagle *et al.*, 2007; Carreiro *et al.*, 2022, 2023). For seabird species that rarely regurgitate freely and/or where their prey is often small, highly digested and difficult to recover for identification through conventional visual taxonomy, molecular approaches

offer the chance to examine dietary differences within and between years. further expanding our knowledge of species foraging ecology.

Seabirds are often considered as climate and ecosystem sentinels due to their capacity to respond to change (Hazen *et al.*, 2019). However, research to quantify the effectiveness of using seabirds as sentinels in the South Atlantic is still needed. The large component of juvenile squid found in the diet of Red-billed Tropicbirds at St Helena suggests further studies could use Red-billed Tropicbirds as indicators of the marine environment to inform on future changes in local juvenile squid abundance and fisheries practices. Furthermore, due to the known sensitivity of tropicbirds to changes in climatic conditions (Le Corre *et al.*, 2003; Castillo-Guerrero, Guevara-Medina and Mellink, 2011), dietary studies could be used to improve our understanding of climate change in tropical marine systems through monitoring the impact of climate change on prey distribution and abundance (Diamond and Devlin, 2003).

7.4.2. Trophic niches

Differences in prey between age groups (adults and chicks (Pedrocchi, Oro and González-Solís, 1996; Davoren and Burger, 1999)) which could only be touched upon in Chapter 6 due to sample size limitations, but also between breeding stages (non-breeding, pre-breeding, incubation and chick rearing) and sexes (male and female (Paiva *et al.*, 2017)) can vary due to differing nutritional requirements (Phillips, Silk, Phalan, *et al.*, 2004; Phillips *et al.*, 2011). This warrants further investigation, as these factors can impact life history traits such as reproductive success. Analysing stable isotopes from seabird feathers, blood and/or prey tissue is another established non-invasive technique for assessing diet composition and quality, providing insights into seabird trophic ecology and predator prey relationships (Phillips *et al.*, 2011; Roscales *et al.*, 2011). For example, Sorensen *et al.*, (2009) found, through stable isotope analysis from Cassin's Auklet (*Ptychoramphus aleuticus*) feathers, evidence of differences in female pre-breeding diet quality and egg size, which may have important consequences for reproductive success. My research shows that dietary analysis could also be used to inform bycatch risk for seabird species (Chapter 6). Examination of dietary preferences in other seabird species at St Helena and Ascension Island could also be used to inform their risk bycatch for those seabird species within the region.

A common foraging strategy employed by many pelagic seabirds is to feed in association with subsurface predators which drive prey to the surface (Ballance and Pitman, 1999; Hamer, Schreiber and Burger, 2002). However, the prey consumed by Red-billed Tropicbirds around St Helena appears to be mainly driven by resource availability within their foraging range (Chapter 6). Verifying Red-billed Tropicbird foraging activities and

behaviour using data gathered by fisheries observers and/or boat surveys in the region is worthy of investigation to improve our understanding of predator prey interactions. Examination of the dietary preferences from multiple seabird species at St Helena may offer more insights into intra and inter-specific competition such as the "halo" effect observed on nearby Ascension Island, where intense competition for food among the large numbers of spatially constrained pelagic predators has resulted in a zone of prey depletion surrounding the island (Weber *et al.*, 2021).

7.4.3. Nest characteristics and monitoring

Further investigation of the thermal microclimate in storm petrel ANC and natural burrows between seasons will help improve our understanding of effects of nest characteristics on breeding performance between the two seasonal *H. helena* populations. Temperature loggers such as Hygrochron iButton have been successfully used in a number of cavity and burrow nesting seabird species, shedding light on aspects of the breeding cycle, attendance and breeding success (Fischer and Taylor, 2018; Michielsen *et al.*, 2019). As chick survival was a major cause of breeding failure in ANCs during the hot season in my study (Chapter 3) indicating that the chambers thermal microclimate and/or thermoregulation of the chick in the warmer hot season may be a causational factor influencing breeding success, such devices could facilitate filling this data gap. Other nest chamber characteristics such as those evaluated for Red-billed tropicbirds (Chapter 2), e.g., nest chamber volume, tunnel length, positioning and substrate, may also prove important components worth further investigation that could lead to improved design and construction of future ANC installations. Findings from which may impact installations in the South Atlantic but may also have wider implications for other burrow nesting seabird species globally.

The utility of motion sensor cameras as a research tool for monitoring nesting seabirds, demonstrated in Chapter 2 & 4 for Red-billed Tropicbirds, has since been developed further as an affordable and reliable method for monitoring smaller seabird species, such as *Hydrobates sp.* (Hereward *et al.*, 2021). Thus, motion sensor cameras could now facilitate continued exploration of possible factors influencing the differing nest survival and chick survival between seasons in *H. helena* observed in Chapter 3. For example, examination of between-season differences in adult nest attendance and provisioning patterns and possibly impacts on chick growth rates could offer insights into the causes of seasonally variation of reproductive performance.

7.4.4. Foraging ecology

Further investigation on the foraging distributions of *H. helena* from other colonies at St Helena as well as Ascension Island would be advantageous in the future, as marine

distributions can differ markedly between colonies at the same locality, and between populations (Awkerman *et al.*, 2014; Quillfeldt *et al.*, 2019). Future tracking studies of *H. helena* should focus on increasing sample sizes, particularly of chick-rearing adults, as the limited sample sizes obtained in my research prohibited comprehensive descriptions of marine distributions between different breeding stages. Sex-specific foraging distributions and behaviour were also not examined in my research, but may provide evidence of additional between season variability, which are an important consideration when assessing the impact of at-sea threats on seabirds (Lewis *et al.*, 2005; Militão, Kürten and Bouwhuis, 2023). Other life-history stages such as non-breeding adults, immatures and juveniles should also be targeted to reduce bias when assessing at sea distributions (Carneiro *et al.*, 2020). Examination of the seasonal differences in *H. helena* non-breeding distributions may also offer more insights and evidence into the dynamics of temporally segregated resource use and its role in sympatric speciation. Given there is little evidence of other segregated populations of seabird species from St Helena (see Diop *et al.*, (2018), Oppel *et al.*, (2015), Chapter 2), combined examination of foraging behaviour and distributions from multiple seabird species at St Helena may offer additional insights into the evolutionary drivers of population segregation. Based on the high mobility observed in *H. helena* at St Helena (Chapter 5) and other seabird species from St Helena and Ascension Island (see Diop *et al.*, (2018), Reynolds *et al.*, (2021), Oppel *et al.*, (2015), Oppel *et al.*, (2017), Weber *et al.*, (2021)), it would be worthwhile completing a comprehensive assessment of important marine areas, based on tracking data from multiple colonies and species in the region to identify marine Important Bird Areas (IBAs) and Key Biodiversity Areas (KBAs) as a key conservation goal.

7.5. Conclusion

The research conducted as part of this thesis represents one of only a few long-term studies conducted in the UKOTs overall and is the most comprehensive study on seabirds at St Helena thus far. In this thesis, I investigated the relatively unknown ecology of both *H. helena* and Red-billed Tropicbirds, therefore my research adds to the body of knowledge relating to subtropical seabird species and provides useful insights into the breeding and foraging ecology of seabirds worldwide. My research highlighted the continued role of introduced predators in the endangerment of island seabird species and gave further evidence that a selected few species such as cats are having detrimental impacts when introduced to island ecosystems. The evidence gathered in this thesis emphasizes the importance of understanding a species flexibility in adjusting to the effects of climate change on ecosystems, in order to predict future changes on life history traits such as reproductive success. This thesis has shown that the foraging dynamics of *H.*

helenae are complex, and that Red-billed Tropicbird foraging in the South Atlantic is specialised, providing results that will be useful for future comparative studies. The insights gathered in this thesis are relevant for scientists working on reproduction, biology and in particular evolutionary theory, as evidence of drivers of evolution by allochrony are scarce. This research can also be used to address the identified species threats through facilitating the feasible conservation and management actions that have been discussed.

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Appendix 1.

Methods used for sexing individual adult Red-billed Tropicbird (*Phaethon aethereus*) and South Atlantic Storm-petrels (*Hydrobates helena*)

I plucked 10-15 mid breast feathers from captured adults. Feathers were placed in paper envelopes and refrigerated until genomic DNA was extracted at Cardiff University, UK, following a Chelex extraction protocol Medeiros Mirra, (2010). DNA was isolated from two feathers from each bird. A small section from the proximal end of the quill and feather shaft were removed and cut into smaller pieces about 50-150 mm in length. These pieces were placed into 1.5ml Eppendorf tubes containing 50 µl sterile water (H₂O). 20 µl Proteinase K (20mg/ml), 20 µl InstaGene™ matrix (Bio-Rad Laboratories, UK) and 10 µl DTT (0.1 M, Thermo Scientific) were then added. All samples were vortexed and then centrifuged at 5000rpm for two minutes, then incubated at 50°C for a minimum of 12 hours followed by heating to 95°C for 15 minutes.

Molecular sex identification was performed using the primer pair 2550F and 2718R following standard protocol described by Fridolfsson & Ellegren (1999), (Table A1.1). DNA quantity and quality were assessed by electrophoresis on 2% agarose gels stained with Syber® Safe (Invitrogen, Eugene, OR, USA) alongside a 100bp molecular weight marker (DNA Ladder, Promega). Both Red-billed Tropicbirds and South Atlantic Storm-petrels amplified bands between 500bp and 700bp. Males being the homogametic sex (ZZ genotype) showed a single band at ca. 700bp, whereas heterogametic females (ZW) showed two fragments at ca. 500bp and 700bp (Figure A1.1).

Positive and negative controls were included for each set of amplifications to avoid incorrect assignments, using DNA extracted from blood samples of known male and female Band-rumped Storm-petrels (*Hydrobates castro*) collected from the Azores islands. A minimum of two negative (no template) reactions were used as negative controls; one from a no-tissue sample extraction, and another using distilled water in the PCR. Of the 141 individual Red-billed Tropicbird samples, 128 were successfully assigned a sex (90.78%), while 13 individuals (9.22%) failed to amplify. Of the 42 individual South Atlantic Storm-petrel samples, 41 were successfully assigned a sex (97.62%), while one individual failed to amplify (2.38%), possibly due to low DNA quality/quantity from the breast feather extracts.

Appendix 1.

References

Fridolfsson, A.-K. and Ellegren, H. (1999) 'A Simple and Universal Method for Molecular Sexing of Non-Ratite Birds', *Journal of Avian Biology*, 30(1), pp. 116–121. doi: 10.2307/3677252.

Medeiros Mirra, R. J. (2010) *The Migration Strategy, Diet & Foraging Ecology of a Small Seabird in a Changing Environment*. Thesis submitted for the degree of Doctor of Philosophy, Cardiff School of Biosciences, Cardiff University, Wales, UK.

Table A1.1. The conditions and reagents for sexing Red-billed Tropicbirds and South Atlantic Storm-petrels at St Helena.

Primers	2550F (5'-GTTACTGATTCGTCTACGAGA-3') 2718R (5'ATTGAAATGATCCAGTGCTTG-3')
PCR reagents	For each 15 µL 5 µL template DNA 0.1 µL 2550F (10 µM) 0.1 µL 2718R (10 µM) 4 µL MgCl ₂ (25 µM) 1.2 µL dNTP (2.5 µM each) 0.7 µL H ₂ O 0.1 µL of GoTaq™ DNA polymerase (5U/ µl; Promega), 3 µL green GoTaq™ reaction buffer (Promega)
PCR profile	95°C for 2 mins 95°C for 30 seconds x 40 cycles 50°C for 45 seconds 72°C for 1 min 30 seconds 72°C for 5 mins °C pause
Gel	2% agarose with Syber® Safe (Invitrogen), 40-120 mins, 120 volts.

Appendix 1.

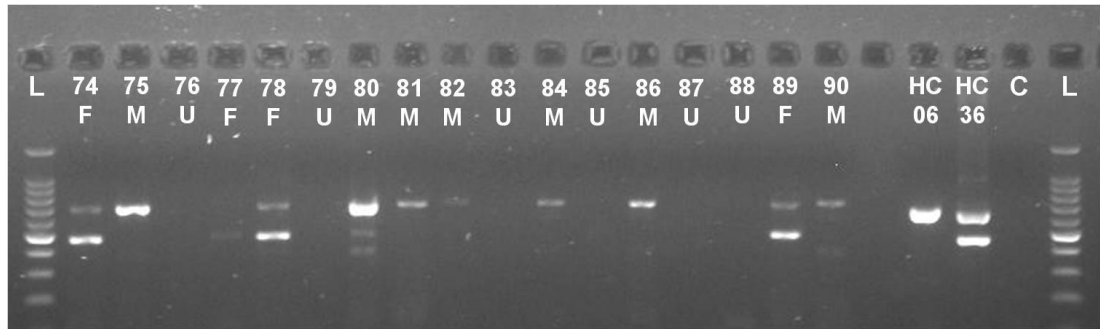


Figure A1.1. Agarose gel picture of PCR products amplified from feather samples of Red-billed Tropicbird (*Phaethon aethereus*) with 2550/2718 primers (Fridolfsson & Ellegren, 1999). F= females, M= males, U= unknown. HC06 and HC36 are a male and female South Atlantic Storm-petrel (*Hydrobates castro*), used as positive controls; C = negative (no template) control, L= 100 bp DNA ladder (New England Biolabs) (bright band: 500bp).

Appendix 2.

Supplementary Information

Table A2.1. Proportion of Red-billed Tropicbird nest monitoring visits to chicks where at least one parent was present with chick at St Helena between 2013-2017.

Chick age (weeks)	Total visits	% parents present
1	265	92.08
2	224	83.04
3	172	68.60
4	134	35.07
5	110	50.00
6	86	33.72
7	76	36.84
8	66	18.18
9	51	23.53
10	39	2.56
11	38	5.26
12	39	2.56
13	35	5.71
14	8	12.50

Table A2.2. Deployment and retrieval of GPS loggers on *H. helena* by breeding stage at deployment and season at St Helena, South Atlantic Ocean.

Breeding stage at deployment	Year	Season	Temporal resolution	Number deployed	Number retrieved (%)	Number of trips obtained
Incubation	2017	Hot	3 hr (2); 2 hr (9)	12	11 (92%)	12L, 2S
	2018	Cool	2 hr	9	4 (44%)	4L
	2018	Hot	4 hr (1); 2 hr (8)	10	9* (90%)	8L, 5S
	2019	Cool	2 hr	18	17** (94%)	14L,16S
	Total			49	41 (83.67%)	38L, 23S
Chick rearing	2017	Hot	1 hr	1	1 (100%)	4L
	2018	Cool	1 hr	2	1 (50%)	4L
	2018	Hot	-	-	-	
	2019	Cool	1 hr	2	1 (50%)	6L
	Total			5	3 (60%)	14L
Grand total				54	44 (81%)	52L, 23S

L = long trips, S = short trips, * all birds with deployed loggers recovered but one logger lost at sea,

**one logger recovered with no usable data, one incubating adult on deployment known to have hatched whilst logger active from nest checks so identified trips split between breeding stages.

Appendix 2.

Table A2.3. Environmental variables considered to explain the spate-temporal variation in long trip foraging locations by *H. helena* tracked with GPS loggers in 2017-2019 at St Helena, South Atlantic Ocean.

Variable name	type	Spatial res	Temporal res	Source
Air temperature (2m above water surface)	atmospheric	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Atmospheric water	atmospheric	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Cloud cover	atmospheric	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Precipitation	atmospheric	0.75 deg	3-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Sea level pressure	atmospheric	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Sunshine duration	atmospheric	0.75 deg	3-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Wind velocity (E-W)	atmospheric	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Wind velocity (N-S)	atmospheric	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Chlorophyll a concentration	oceanographic	4.64 km	monthly	https://oceandata.sci.gsfc.nasa.gov/VIIRS-SNPP/Mapped/Monthly/4km
Current meridional velocity at surface	oceanographic	0.33 deg	5-days	https://doi.org/10.5067/OSCAR-03D01
Current zonal velocity at surface	oceanographic	0.33 deg	5-days	https://doi.org/10.5067/OSCAR-03D01
Sea surface temperature	oceanographic	0.75 deg	daily	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Euphotic depth	oceanographic	4.64 km	8-days	https://oceandata.sci.gsfc.nasa.gov/VIIRS-SNPP/Mapped/8-Day/4km
Wave height	oceanographic	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc
Wave direction	oceanographic	0.75 deg	6-hourly	http://apps.ecmwf.int/datasets/data/interim_full_daily/?levtype=sfc

Appendix 2.

Table A2.4. Summary of correlation between environmental predictor variables selected to determine their influence on the foraging patterns of *H. helena* at St Helena. Bold typeface indicates significant correlation. SST = sea surface temperature, Chla = Chlorophyll *a* concentration.

	Sea level pressure	Sunshine	Total cloud cover	Wave Height	Wave direction	Chla	Wind speed	Current speed	SST	Air Temperature	Atmospheric water
Sea level pressure	-	-0.04	-0.05	0.28	0.11	-0.36	0.08	0.03	0.11	-0.05	-0.30
Sunshine	-0.04	-	-0.20	-0.01	-0.02	-0.01	0.01	0.03	-0.07	0.16	0.04
Total cloud cover	-0.05	-0.20	-	0.12	-0.32	-0.06	0.30	0.15	-0.39	-0.42	0.18
Wave Height	0.28	-0.01	0.12	-	0.11	-0.10	0.44	0.00	0.01	0.08	0.33
Wave Direction	0.11	-0.02	-0.32	0.11	-	0.30	-0.57	-0.12	0.26	0.11	-0.21
Chla	-0.36	-0.01	-0.06	-0.10	0.30	-	-0.18	-0.10	-0.02	-0.09	-0.04
Wind speed	0.08	0.01	0.30	0.44	-0.57	-0.18	-	0.08	-0.16	0.00	0.35
Current speed	0.03	0.03	0.15	0.00	-0.12	-0.10	0.08	-	-0.27	-0.21	-0.01
SST	0.11	-0.07	-0.39	0.01	0.26	-0.02	-0.16	-0.27	-	0.84	-0.11
Air temperature	-0.05	0.16	-0.42	0.08	0.11	-0.09	0.00	-0.21	0.84	-	0.12
Atmospheric water	-0.30	0.04	0.18	0.33	-0.21	-0.04	0.35	-0.01	-0.11	0.12	-

Appendix 2.

Table A2.5. Percent overlap of kernel densities during long trips for *H. helena* at St Helena tracked with GPS loggers. Overlap is compared between seasons, sexes, breeding stages and years. The degree of overlap is indicated by shading from lower (pink) to higher (dark pink). We averaged the overlap values for each category (mean) and calculated the raw overlap of all locations for each category (overlap total).

			50%	75%	95%
Hot vs. Cool	Breeding stage	Incubation	16.403	18.843	36.058
		Chick rearing	54.415	39.622	38.400
	Sex	male	25.759	21.063	40.273
		female	21.583	21.829	31.039
	Year	First	23.625	14.635	15.508
		Second	14.492	22.343	46.625
	Mean		26.046	23.056	34.650
	Overlap Total		29.635	27.561	41.124
Female vs. Male	Breeding stage	Incubation	47.326	67.804	77.137
		Chick rearing	22.616	18.191	18.159
	Year	First	25.244	19.970	32.429
		Second	37.963	68.529	92.493
	Season	Hot	48.812	62.356	68.821
		Cool	53.025	80.305	81.194
	Mean		39.164	52.859	61.706
	Overlap Total		60.977	67.048	69.439
Incubation vs. Chick rearing	Sex	male	12.679	11.856	16.700
		female	20.016	22.237	26.325
	Year	First	28.001	22.952	29.077
		Second	15.869	21.368	28.540
	Season	Hot	20.489	26.625	28.836
		Cool	28.222	35.106	39.567
	mean		20.879	23.357	28.174
	Overlap Total		29.568	33.750	38.168
First year vs. Second Year	Breeding stage	Incubation	54.898	54.500	69.515
		Chick rearing	36.888	32.772	45.663
	Sex	male	44.666	55.606	80.556
		female	40.825	43.561	59.186
	Season	Hot	43.368	56.721	67.302
		Cool	49.066	72.453	84.055
	mean		44.952	52.602	67.713
	Overlap Total		57.033	63.175	73.462



Figure A2.1. South Atlantic Storm-petrel (*Hydrobates helena*) with retrieved GPS logger (photo: St Helena Government).

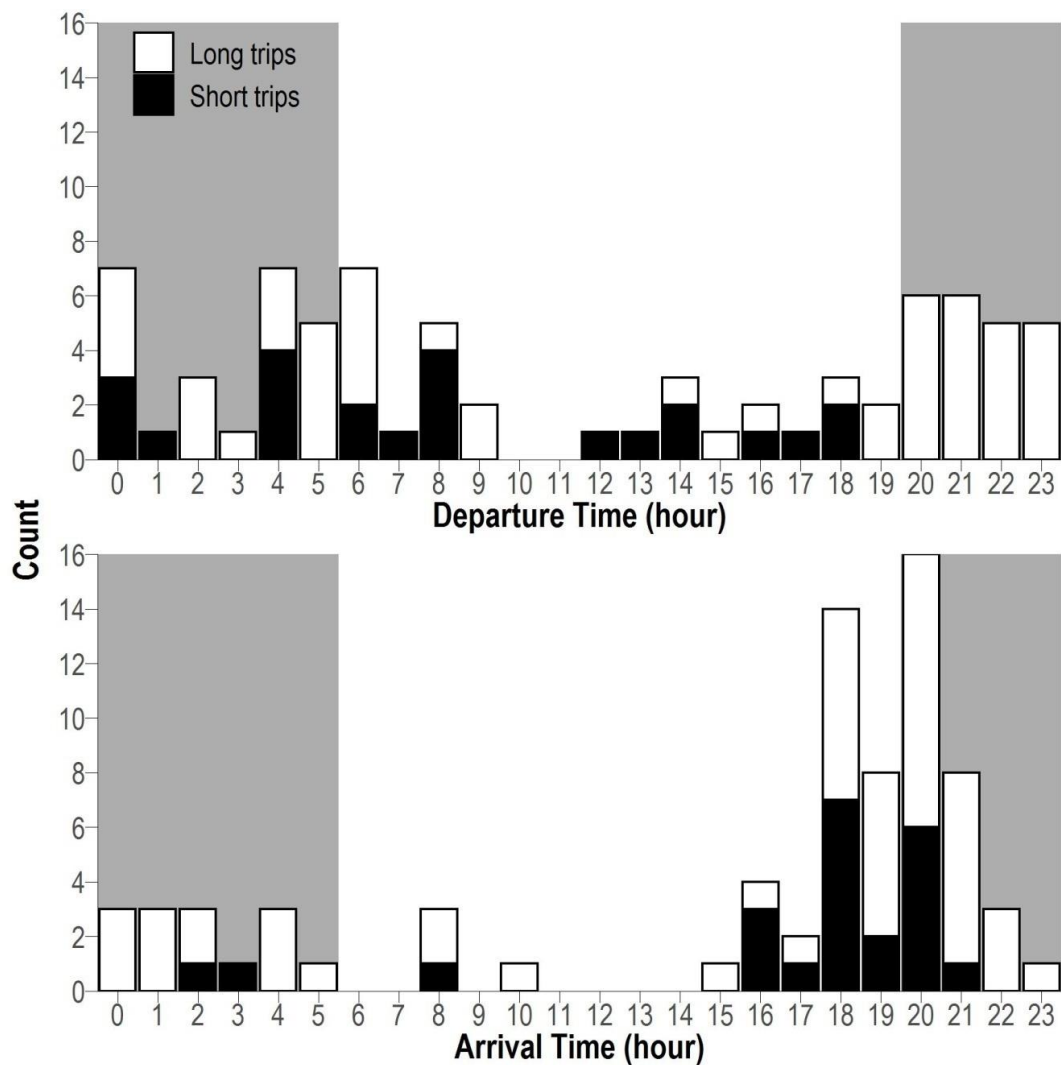


Figure A2.2. Frequency of departures (top panel) and arrivals (bottom panel) of South Atlantic Storm-petrel (*Hydrobates helena*) determined by GPS tracking data; long (white box) and short (black box) trips rounded to the nearest hour. Grey shaded areas indicate night using mean sunset and sunrise times; white shaded areas indicate daytime

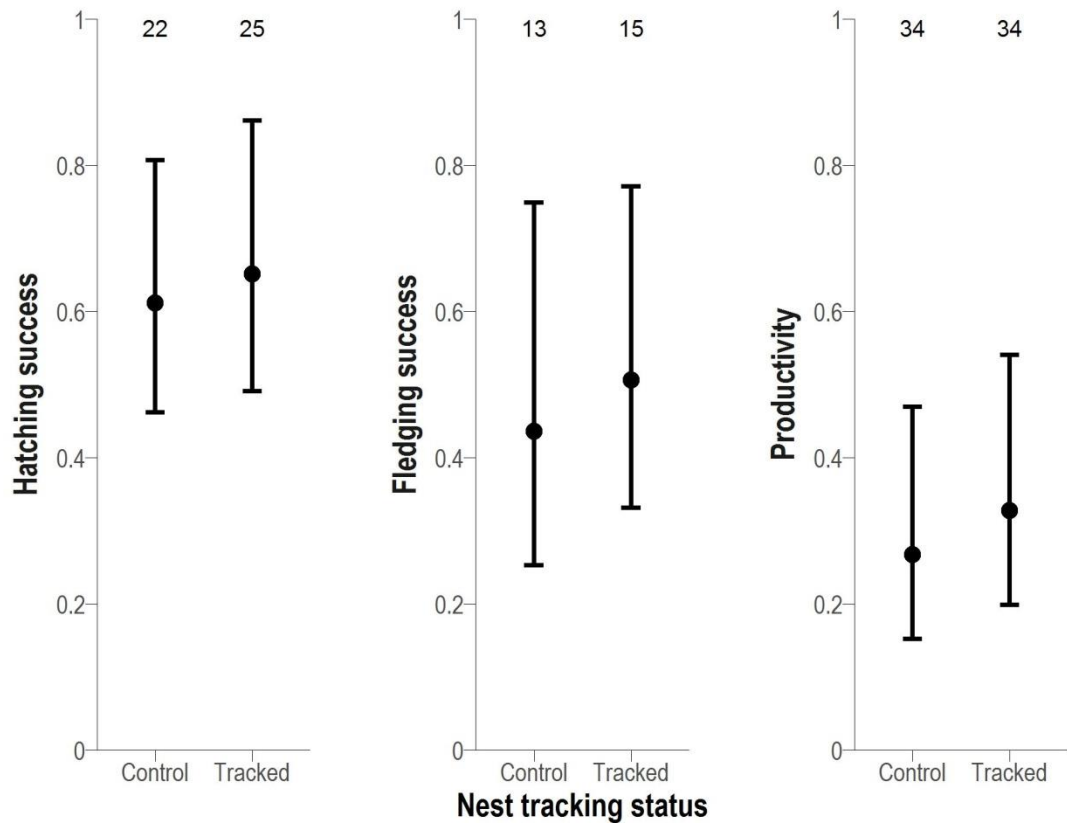


Figure A2.3. Relationship between estimated breeding success during hatching, fledging and overall productivity of *H. helena* from control nests and nests used during the tracking study. Estimated success results are based on 34 nests used for tracking and 34 control nests pooled across 2017-2019. The points represent the estimated breeding success values, and whiskers represent the 95% confidence intervals.

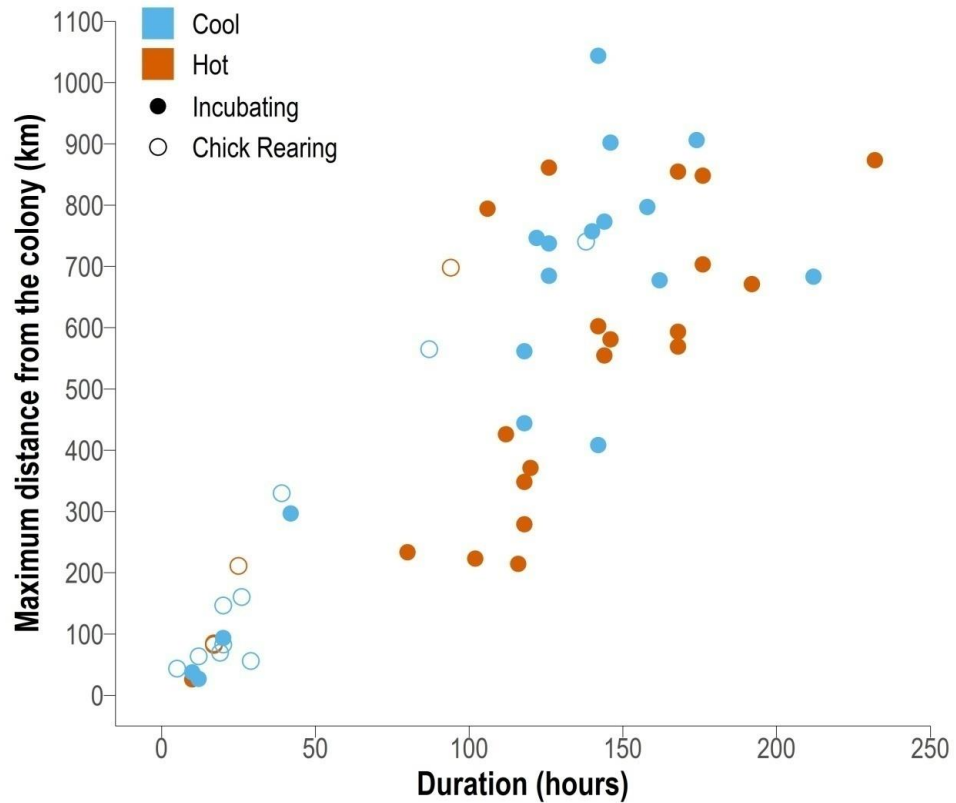


Figure A2.4 Relationship between maximum distance travelled from the colony and foraging trip duration in long trips of South Atlantic Storm-petrels (*H. helena*) tracked with GPS loggers.

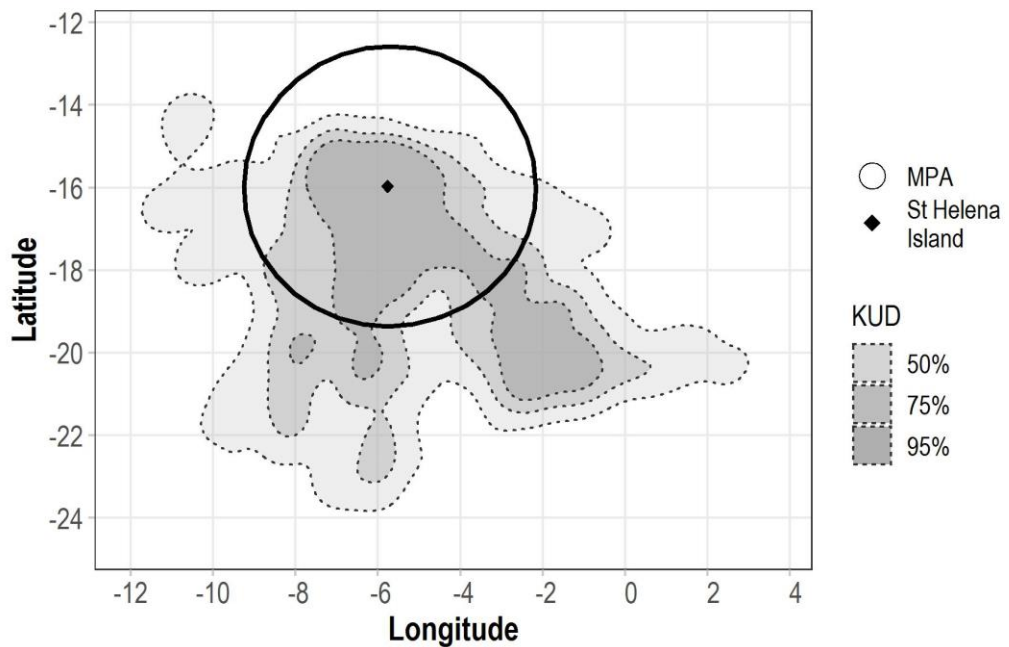


Figure A2.5. Utilisation distribution of South Atlantic Storm-petrels (*H. helena*) at St Helena during long trips. Polygons represent the 95, 75, and 50% kernel utilisation distributions (KUD), respectively. The black diamond indicates the location of St Helena Island, and the black line indicates the 200 nm Marine Protected Area (MPA).