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WHITE-FACED STORM PETRELS IN THE NORTHEAST ATLANTIC: CONTRIBUTIONS TO THE KNOWLEDGE OF THEIR BEHAVIOUR, ECOLOGY AND CONSERVATION

Maria Saldanha Alho

This thesis is submitted in partial fulfilment for the degree of PhD in

Behavioural Biology

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"– Adeus – despediu-se a raposa. – Agora vou-te contar o tal segredo. É muito simples: só se vê bem com o coração. O essencial é invisível para os olhos…
– Foi o tempo que tu perdeste com a tua rosa que tornou a tua rosa tão importante.
– Os homens já não se lembram desta verdade – disse a raposa. – Mas tu não te deves esquecer dela. Ficas responsável para todo o sempre por aquilo que cativaste. Tu és responsável pela tua rosa…"

– Antoine de Saint-Exupéry,
Le Petit Prince

Aos meus pais,
pelo apoio incondicional.

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RESUMO

Compreender o comportamento alimentar e reprodutor dos painhos, o grupo mais pequeno dos Procelariiformes, é crucial para compreender a sua ecologia e eficaz conservação. Apesar da sua ampla distribuição, estas aves têm sido pouco estudadas devido a desafios como o seu tamanho pequeno, comportamento noturno e locais de reprodução remotos. Dispositivos de seguimento miniaturizados começaram a fornecer informações sobre a sua distribuição e comportamento no mar, mas ainda há muito a descobrir sobre a sua dieta, comportamento, movimentos, rotas de migração e áreas de invernada.

Esta tese de doutoramento concentrou-se principalmente na recolha e resumo de dados existentes sobre o comportamento alimentar e reprodutor dos painhos. Focou-se especialmente no calca-mar *Pelagodroma marina*. O estudo inclui uma análise do comportamento da procura de alimento e preferências alimentares do calca-mar, uma investigação de uma colónia extinta e uma avaliação da utilidade potencial de ninhos artificiais como ferramenta de investigação durante a época de reprodução.

A minha revisão resume o conhecimento existente sobre o comportamento alimentar e reprodutor dos painhos, destacando a escassez de investigação nesta área e sublinhando as numerosas questões ecológicas não respondidas sobre a maioria das espécies de painhos, indicando a necessidade de futuras investigações.

Pela primeira vez, investiguei o comportamento de procura de alimento do calca-mar na ilha Selvagem Grande (NE Atlântico), utilizando dispositivos GPS de 1g ao longo de dois anos consecutivos, durante os períodos de incubação e criação de crias. Foi também analisado amostras de fezes das crias através de DNA metabarcoding para caracterizar a sua dieta e examinou-se os níveis de mercúrio nas penas do corpo das crias. Os calca-mares partiram da colónia sem uma preferência clara de direção e com um uso predominante de águas oceânicas profundas. Durante a criação de crias, estas aves exibiram maior atividade noturna, alimentando-se principalmente de presas mesopelágicas, conforme refletido pela dieta e pelos seus níveis relativamente elevados de mercúrio nas penas.

Esta tese apresenta as primeiras informações sobre as populações de aves marinhas extintas na ilha de Santa Luzia, em Cabo Verde. A presença abundante de subfósseis de aves marinhas sugere que a ilha foi um importante local de reprodução para três espécies de Procelariiformes, especialmente para o calca-mar. A datação por radiocarbono sugere que a colónia tenha desaparecido no início do século XX, possivelmente devido à presença humana e de animais domésticos. No entanto, após a erradicação de gatos assilvestrados, a ilha possui potencial para a recuperação das colónias de aves marinhas, uma vez que as populações extintas eram muito maiores do que as atuais em Cabo Verde.

Finalmente, explorei a eficácia de ninhos artificiais para o calca-mar, com o objetivo de melhorar o monitoramento de aves reprodutoras, facilitar estudos durante a época de reprodução e conservação a longo prazo para painhos que nidificam em cavidades. Ninhos artificiais instalados dentro de ninhos naturais pré-existentes mostraram elevadas taxas de ocupação (83% em dois anos) e maior sucesso reprodutivo em comparação com ninhos naturais. O sucesso de eclosão foi maior em ninhos artificiais (>70%) em comparação com ninhos naturais. Foi observado abandono de ovos em ambos os tipos de ninhos, e a predação por lagartixas da Madeira foi menor em ninhos artificiais, sugerindo que oferecem uma melhor proteção, especialmente até à eclosão.

Esta tese apresenta novos dados sobre o comportamento e a ecologia do calca-mar, com potenciais implicações para entender o comportamento de outros painhos, destacando a importância de estudos a longo prazo e paleoecologia para ações de conservação.

ABSTRACT

Understanding the foraging and breeding behaviour of storm petrels, the smallest group among Procellariiformes seabirds, is crucial to comprehend their ecology and effective conservation. Despite their wide distribution, storm petrels have been relatively understudied among seabird families. This limited research is primarily due to several challenges, including their small size, cryptic nocturnal behaviour, and remote breeding locations. Miniaturized tracking devices have started to provide insights into their marine distribution and behaviour, yet, there is still much to learn about their foraging behaviour, trophic ecology, movement patterns, migration routes, and wintering areas.

This doctoral thesis has primarily concentrated on gathering and summarizing existing data regarding the foraging and breeding behaviours of storm petrels. It delves particularly into the White-faced Storm Petrels *Pelagodroma marina*, a small oceanic seabird. The study encompasses an analysis of White-faced Storm Petrels foraging behaviours and dietary preferences, an investigation of an extinct colony, and an assessment of the potential utility of artificial nests as a research tool during the breeding season.

My review summarizes the existing knowledge on colonial behaviour, foraging and diet preferences in several colonies worldwide, and highlights the scarcity of research in this area and underscores the numerous unanswered ecological questions concerning most storm petrel species, indicating the need for future investigations.

For the first time, I investigated the foraging behaviour of White-faced Storm Petrels in the Selvagem Grande island, (NE Atlantic), using 1g-GPS devices over two consecutive years, during the incubation and chick rearing periods. The research also analyzed the chick fecal samples through DNA metabarcoding to characterize their diet and examined mercury levels in chick body feathers. White-faced Storm Petrels departed from the colony without a clear preference in direction and with a predominant use of deep oceanic waters. During chick rearing, these birds displayed higher nocturnal activity, primarily feeding on mesopelagic prey, as reflected by dietary information and their relatively high feather mercury levels.

This thesis offers the first insights into the extinct seabird populations on the uninhabited Santa Luzia Island, in Cabo Verde. The high abundance of subfossil petrel bones found in the sampling area suggests that the island was a significant breeding site for three seabird species, especially the White-faced Storm Petrel. Radiocarbon dating of bone remains suggests that the colony likely disappeared in the early 20th century, possibly due to human and domestic animal presence. The island, after feral cat eradication, holds potential for seabird restoration, as the extinct populations were once much larger than current ones in Cabo Verde.

Finally, I explored the effectiveness of artificial nests for White-faced Storm Petrels, aimed at improving monitoring of breeding birds and facilitating long-term breeding and conservation studies for burrow-nesting petrels. Artificial nests installed within existing burrows showed high occupancy rates (83% in two years) and higher breeding success compared to natural nests. Hatching success was higher in artificial nests (over 70%) compared to natural nests. Egg neglect was observed in both types of nests, and predation by Madeiran Wall Lizards was lower in artificial nests, suggesting they offer better protection, especially until hatching.

The thesis provides novel data into the behaviour and ecology of White-faced storm petrels, shedding light on behaviours of other storm petrel, and emphasizing the importance of long-term studies and paleoecology for conservation action.

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CHAPTER 1

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GENERAL INTRODUCTION

Understanding the distribution and abundance of species is crucial for ecological comprehension and effective conservation management. However, for storm petrels, the smallest seabirds belonging to the Procellariiformes, obtaining such basic information is challenging due to their elusive behaviour and ecology. Moreover, most ecological research tends to rely on short-term local field studies, lacking the broader historical context (Jackson et al., 2001).

Storm petrels are a diverse group of small pelagic seabirds, widely distributed across the world's oceans, with 27 known species belonging to six genera from two main families: Oceanitidae (Southern storm petrels) and Hydrobatidae (Northern storm petrels). These species exhibit a wide range of geographical distributions, ranging from single-island endemics to species-complexes that span entire oceans (Brooke, 2004a; Warham, 1990). These seabirds are among the most threatened globally (Croxall et al., 2012), and invasive species on islands represent one of their greatest threats (Croxall et al., 2012; Lees et al., 2022; Veitch et al., 2011). The diminutive size of storm petrels makes them highly vulnerable to predators, particularly on remote islands where they nest in crevices or burrows and come to land under darkness (Davis, 1957; Warham, 1990). As a consequence, obtaining accurate counts of breeding storm petrels is notoriously difficult, leading to imprecise population estimates (Mitchell et al., 2004). In cases where population declines have been observed, the exact drivers behind these declines sometimes remain unknown (e.g., Wilhelm et al., 2019). In addition to predation by invasive species, storm petrels face a range of other important threats, including light pollution (e.g., offshore light attraction) (e.g., Lieske et al., 2019; Rodríguez et al., 2017; Ronconi et al., 2015), climate change effects (e.g., spatial shift and depletion in prey items) (Ausems et al., 2023; Mauck et al., 2018,) and increased populations of native avian predators like gulls, skuas, and owls at breeding sites (e.g., Sanz-Aguilar et al., 2009; Votier et al., 2006). Disease impacts on these birds remain unclear, though infectious diseases have affected other Procellariiform species (Weimerskirch, 2004). Furthermore, storm petrels are also highly exposed to various contaminants in marine environments (Burger & Gochfeld, 2004; Furness & Camphuysen, 1997), including mercury (Bond & Diamond, 2009; Pollet et al., 2017; Pollet et al., 2023; Quillfeldt et al.,

2023) and microplastics (Clark et al. 2023; De Pascalis et al., 2022; Furtado et al., 2016, Krug et al., 2021; Nam et al., 2021; Youngren et al., 2018), owing to their long lifespan and lower trophic position in marine food webs compared to larger seabirds.

Despite their wide distribution, storm petrels have been among the lesser-known bird families. Limited research has been conducted on their at-sea behaviour, habitat usage, and pelagic ecology, mainly due to the challenges of studying them in their remote oceanic habitats (Ainley, 2005; Crossin, 1974; del Hoyo, et al. 1992; Howell, 2012). Storm petrels spend a significant part of their lives at sea, and their marine distribution and behaviour is difficult to study. Furthermore, their small size renders them challenging to detect in aerial or vessel-based surveys, making it crucial to use miniaturized tracking devices to advance our understanding of their marine distributions and behaviours (Yoda, 2019). Tracking these birds has been a challenge historically, and as a result, there is a considerable knowledge gap regarding their spatial ecology. This includes aspects such as foraging behaviour, movement patterns, migration routes, and wintering areas. This knowledge is particularly important as anthropogenic pressures on the marine environment continue to escalate. Understanding the at-sea behaviour and spatial utilization of pelagic seabirds is crucial to comprehending their role in ocean ecosystems and has become increasingly important for informing marine spatial planning.

Storm petrels, as lower trophic level consumers primarily feeding on small fish, squid and small crustaceans, have the potential to act as rapid indicators of environmental changes, especially when compared to larger seabird species (Grémillet et al., 2015). Additionally, meaning changes in their populations can signal unseen environmental alterations, such as pollution events (Mallory et al., 2010; Sydeman et al., 2021). As a result, studies on diet and feeding ecology on storm petrels provides valuable insights for monitoring the overall health of marine ecosystems.

Burrow-nesting seabirds, such as storm petrels, are challenging to study and sample in their breeding colonies, due to the delicate nature of their nesting sites. Monitoring these birds involves various methods, some of which can be invasive, potentially disturbing the nest and affecting the birds' breeding success. Non-invasive techniques may not be suitable for long-term studies on small seabirds. Invasive methods like burrow-scopes or manually inspecting nest contents can be effective but may also cause disturbance and habitat damage. Altering nest access for tracking or sampling purposes can further impact the burrow's suitability and increase risks to the birds and their nesting environment.

Additionally, the impacts of ancient civilizations and past human activities on seabird ecosystems remain largely unknown, preventing the full comprehension of cumulative impacts on seabird populations before modern monitoring efforts. Long-term monitoring of seabirds is essential to accurately identify the drivers of change, considering their extended lifespan. A solid knowledge of storm petrels' breeding and foraging behaviour, ecology and long-term historical trends provides essential insights into the population and community dynamics of storm petrels, enabling informed decisions for their conservation and management (Clutton-Brock & Sheldon, 2010; Croxall et al., 2012; Dias et al., 2019; Paleczny et al., 2015; Rodríguez et al., 2019).

1.1. THE BEHAVIOUR OF STORM PETRELS

Storm petrels have specific preferences for marine habitats, nesting sites, and migratory behaviour, resulting in ecological segregation among species (Ainley, 2005; del Hoyo et al., 1992; Spear & Ainley, 2007). However, due to their small size and cryptic behaviour, understanding their habits and behaviour has been difficult, especially in relation to foraging behaviour. These seabirds possess physiological and morphological adaptations that enable them to exploit diverse prey sources in different ways. The specifics of foraging trips vary by species and oceanic habitats, influenced by their physical characteristics and foraging strategies. Distinct species of storm petrel exhibit diverse foraging behaviours and consume a range of prey types (Monteiro & Furness, 1997; Spear & Ainley, 2007).

Several species of storm petrels exhibit a distinct foraging behaviour known as "pattering", where they appear to walk on the water's surface. In fact, this behaviour has given rise to the term "petrel," derived from the biblical story of Saint Peter walking on water (Lockley, 1983). While this behaviour is common within storm petrels, its prevalence varies among species (Sausner et al., 2016). In addition to pattering, other foraging behaviours, including shallow dives, have been documented (Albores-Barajas et al., 2011; Bried, 2005; Harrison et al., 2013). Moreover, storm petrels are also known to possess an enhanced sense of smell, which also exhibits variation among species.

Different olfactory abilities or adaptations are likely to play a role in the diverse foraging strategies employed by different species in various situations.

Storm petrels predominantly forage offshore and over pelagic waters, often above or beyond the continental shelf. They are mostly surface foragers, feeding on prey available at the ocean's surface, using various foraging techniques, such as snatching prey from the surface or performing sea-anchor soaring. Storm petrel diet mainly comprises small crustaceans, fish, and cephalopods, but detailed information is limited. Prior research on storm petrels' distribution was often conducted through ship surveys, providing foundational knowledge. Yet, technological miniaturization now enables the study of foraging behaviours of smaller species like storm petrels, which were once challenging or impossible to observe (e.g., Hedd et al., 2018; Rotger et al., 2020).

Seabird colonies, often characterized by noise and activity due to colonial behaviours, necessitate effective communication (Warham, 1990). Storm petrels, like other seabirds, have evolved distinct physiological and sensory adaptations in response to their pelagic and colonial lifestyles. They select their nesting habitat by utilizing public information, which might include visual, auditory, and olfactory cues from conspecific breeding individuals (Schreiber & Burger, 2001).

Despite the lack of studies, evidence points to ecological distinctions among species, including preferences for specific oceanic conditions (Spear & Ainley, 2007), nest-site choices (Ainley, 2005), migratory behaviour (del Hoyo et al., 1992), and breeding timing (Monteiro & Furness, 1998). Moreover, it is considered that morphological differences between the two families (Oceanitidae and Hydrobatidae), correspond to ecological variations, especially in terms of foraging behaviour (Sausner et al., 2016).

1.2. CASE STUDY: THE WHITE-FACED STORM PETREL

1.2.1 TAXONOMY, MORPHOLOGY AND DISTRIBUTION

The White-faced Storm Petrel *Pelagodroma marina* is a small burrow-nesting seabird, a unique member of the monotypic genus *Pelagodroma*, belonging to the Hydrobatidae family, with six subspecies found in the temperate, subtropical, and tropical regions of Atlantic, Pacific, and Indian Oceans in both Hemispheres (del Hoyo et al., 1992). These small-sized seabirds with particularly long legs, typically weigh between 40 to 70 gram and measure 18 to 21 centimeter in length, with a wingspan spanning 42 to 43 centimeter (Brooke, 2004; Marchant & Higgins, 1990).

During the breeding season, White-faced Storm Petrels establish large colonies in the southern hemisphere, occupying remote oceanic islands like Tristan de Cunha (St Helena), as well as on many islands around Australia and New Zealand, like Chatham Islands (BirdLife International, 2023a; del Hoyo et al., 1992). In the northern Atlantic, the breeding populations are relatively smaller and restricted to the Selvagens, Canary, and Cabo Verde islands (Campos & Granadeiro, 1999; del Hoyo et al., 1992; Rodríguez et al., 2003, Silva et al., 2015). The global population of the European subspecies *Pelagodroma marina hypoleuca* is mostly confined to the Selvagens Islands in the North-east Atlantic, except for a few breeding pairs in the Canary Islands (Campos & Granadeiro, 1999; Catry et al., 2010; Rodríguez et al., 2003; Silva et al., 2015). An estimated 61,000 breeding pairs were recorded in the Selvagens archipelago in 1996, with 36,000 pairs specifically estimated on Selvagem Grande during the same year (Campos & Granadeiro, 1999).

1.2.2. FORAGING BEHAVIOUR AND DIET

White-faced Storm Petrels are solitary-feeders and surface foragers, possessing a distinct flight behaviour and morphology, characterized by wide wings and notably long legs and feet (Marchant & Higgins, 1990). When feeding, they often exhibit a unique flight pattern, hopping along the water surface while facing the wind with wings extended. This behaviour is commonly known as "pattering" (Spear et al., 2007; Warham, 1990; Watson et al., 1986). Their diet mainly comprises small fish, pelagic crustaceans, and surface plankton (Brooke, 2004a,2004b; Imber, 1984; Marchant & Higgins, 1990; Spear et al., 2007). They appear to be opportunistic feeders, consuming a diverse array of Myctophidae and other mesopelagic fishes both during the night and day, as well as pelagic fishes, crustaceans, and other non-cephalopod invertebrates (Spear et al., 2007). Seabirds with a specialization in mesopelagic prey are known for their frequent foraging in offshore and oceanic waters, particularly during nighttime (Brooke & Prince, 1991; Spear et al., 2007; Warham, 1990). Mesopelagic fish and cephalopods exhibit diel vertical migrations, which make them accessible to shallow diving seabirds during the night

(Gjøsaeter & Kawaguchi, 1980; Watanabe et al., 1999). However, so far there is no comprehensive information about the feeding ecology of White-faced Storm Petrels from the North Atlantic.

Previous studies on White-faced Storm Petrels have primarily focused on their breeding biology, and their at-sea distribution remains largely unknown (Campos & Granadeiro, 1999; Menkhorst et al., 1984; Richdale, 1943-1944; Underwood & Bunce, 2004). Some ship-based observations suggest that they forage over continental shelves (Cramp & Simmons, 1997; Rankin & Duffey, 1948; Spear et al., 2007; Warham, 1990). In contrast, an analysis of stable carbon isotopes in toe-nails from the Selvagem Grande population indicates that these birds probably forage over the deep ocean around the Selvagens Islands, rather than feeding close to the African coast (Furtado et al., 2016).

1.2.3 THREATS

Although there are indications of a decreasing population trend, the species is currently classified as being of "Least Concern" under the IUCN Red List Classification (BirdLife International, 2023). Until the beginning of the 2000s, predation by house mice *Mus musculus* significantly contributed to breeding failure in the Selvagem Grande colony. However, the impact of house mice on the White-faced Storm Petrel's population dynamics seemed irrelevant given the high breeding success at the time (Campos & Granadeiro, 1999). There are currently no house mice on the island since they were successfully eradicated in 2002. On these islands, White-faced Storm Petrels face significant predation from yellow-legged gulls, resulting in thousands of them being consumed annually (Catry et al., 2010; Matias & Catry, 2010).

On a global scale, the main threats to their breeding colonies seem to be related to the accidental introduction of predators (rats, mice, cats), which can have a significant local impact through predation on eggs, chicks, and adult birds (Baker et al., 2002; Bell & Bell, 2003; del Hoyo el al., 1992; Semedo et al., 2020). Trampling of nests by people or livestock can also have a considerable impact (del Hoyo el al., 1992). Furthermore, research conducted in the South Atlantic and in the Pacific Oceans has reported a high occurrence of plastic ingestion in this species (e.g., Day et al., 1985; Ryan, 2008; Spear et al., 1995), and more recent studies have also documented plastic ingestion on the Selvagem Grande island colony (Furtado et al., 2016). Seabirds, like the White-faced

Storm Petrel, which are thought to heavily depend on mesopelagic prey, also tend to exhibit higher mercury concentrations compared to species with an epipelagic diet (Carravieri et al., 2018; Furtado et al., 2019, 2021; Kim et al., 1996; Monteiro & Furness 1995). However, no specific study on potential deleterious effects of such contaminaton has yet been conducted on this particular species.

1.2.4 BREEDING BEHAVIOUR AND LIFE HISTORY

Typically, colonies of White-faced Storm Petrels are situated in flat areas with shallow and friable soil, providing the perfect conditions for them to dig their burrows (Marchant & Higgins, 1990). These burrows are excavated at densities ranging from 1.5 to 4 burrows per square meter in relatively shallow ground (Brooke, 2004; Gillham, 1963). The breeding cycle of the White-faced Storm Petrel in the North Atlantic begins in March, with birds returning to their colonies approximately six to seven weeks before laying their eggs (Brooke, 2004). The egg-laying phase lasts until early June and by mid-August all chicks have fledged (Campos & Granadeiro, 1999). Both parents participate in the incubation process, taking turns sitting on the eggs for an average duration of four to five days (Richdale, 1965). For the Atlantic White-faced Storm Petrels *P. m. hypoleuca*, the incubation period lasts around 54 days (but is highly variable due to frequent egg-neglect) and chick rearing varies between 55 and 67 days (Campos & Granadeiro 1999, Richdale, 1965, Underwood & Bunce, 2004). A poor breeding synchrony within the colony is also manifested in this species, with 76 days passing between the discovery of the first and last clutches, as it is for most species of this family (Campos & Granadeiro 1999; Warham 1990). Pre-breeding birds probably return to colonies for the first time at around three years old (Menkhorst et al., 1984), two to three years before breeding (Marchant & Higgins, 1990). The specific life span of White-faced Storm Petrel remains uncertain, although the oldest recorded individual from Australia was 16 years old (Menkhorst et al., 1984).

1.3. UNDERSTANDING THE IMPACTS OF HISTORICAL EVENTS

Species on islands are particularly vulnerable to extinction (Carlquist, 1965; Quammen, 1996; Sodhi et al., 2009) primarily because of the lower resilience to the introduction of invasive species and the impacts of climate change (Brooke et al., 2017; Manne et al., 1999). Islands around the world often support large seabird colonies (Belopol'skii, 1957; Croxall & Prince, 1980; Hunter et al., 1982; Pearson, 1968), however, over the past centuries, numerous seabird species have experienced population declines or total extinctions, often linked to the Polynesian and the European expansion (Steadman, 2006). Studies in paleornithology suggest that most seabird extinctions occurred in insular ecosystems (Olson & James, 1982; Quammen, 1996; Rando & Alcover, 2008, 2010; Steadman, 2006; Worthy & Holdaway, 2002). Seabirds are especially vulnerable to human-induced disturbances like habitat destruction, hunting, and the introduction of predators (Croxall et al., 2012; Dias et al., 2019).

During the Holocene, more than 20 documented seabird extinctions have occurred on islands worldwide, and many others may have gone unnoticed (Scofield, 2009; Steadman, 2006; Tyrberg, 2009). Seabird extinctions resulting from the arrival of human explorers and settlers are well-documented (Blackburn et al., 2004; Croxall et al., 2012). Notably, two flightless species, the Great Auk *Pinguinus impennis* in the North Atlantic and the Spectacled Cormorant *Urile perspicillatus* in the North Pacific, went extinct due to human interference and overhunting (Montevecchi & Kirk, 2020; Watanabe et al., 2018). The significant impacts of human exploration on seabird populations were not limited to flightless species. Several seabirds, which shared behavioural similarities with storm petrels, also faced extinction as Europeans explored the Atlantic such as Saint Helena Petrel *Pseudobulweria rupinarum* and Lava Shearwater *Puffinus olsoni* (IUCN, 2023).

1.3.1. SEABIRD FOSSILS AS A TOOL FOR INFERRING THE PAST

Unraveling the impacts of past civilizations on seabird colonies can be challenging. While the effects of present-day anthropogenic activities on seabirds are increasingly being studied, our understanding of historical human impacts on marine ecosystems remains limited. Seabirds, as a group, hold significant promise for understanding past environmental changes. Seabird fossils and subfossils offer valuable yet underexplored insights into historical population and community dynamics, as well as biogeographical patterns and modern-day ecosystems (Steadman, 2006; Steadman & Olson, 1985; Warheit, 2002). Fossil seabirds are particularly valuable for studying how fauna responded to such changes because they are abundant in collections and easily identifiable from fragmentary remains. By studying these fossils, researchers can gather information about coexisting species during specific time periods and in particular geographic areas. Additionally, these fossils elucidate on the original species composition of regions, contributing to a deeper understanding of past environments and ecological interactions (Steadman, 2006). These records provide valuable information on large temporal and demographic scales involving thousands of individuals, which cannot be easily obtained through experimental designs. Moreover, fossil assemblages of extinct birds offer guidance for local conservation efforts aimed at restoring ecosystem function and processes through reintroduction initiatives (Barnosky et al., 2017; Wood et al., 2017).

1.3.2. HISTORICAL RECORDS IN THE NORTH ATLANTIC

Historically, the colonization of various archipelagos in the North Atlantic, including the Azores, Madeira, Canary, and Cabo Verde, led to a significant reduction in seabird populations (Monteiro et al., 1996a; Saavedra et al., 2018; Vasconcelos et al., 2015). These five archipelagos harbor similar seabird assemblages (Monteiro et al., 1996a). Several seabird fossils have been documented in these archipelagos (Alcover & McMinn 1995; Monteiro et al., 1996a; Pieper, 1985; Rando & Alcover, 2008, 2010). Notably, the fossil record of the Canary Islands indicates a significant decline in the original Procellariiformes community, with two confirmed extinct species thus far, the Dune Shearwater *Puffinus holeae* and the Lava Shearwater *Puffinus olsoni* (McMinn et al., 1990; Rando 2002; Rando & Alcover 2008, 2010; Walker et al., 1990). However, there is limited research on the seabird fossils of Cabo Verde, with only one study referencing the island of Sal (Boessneck & Kinzelbach, 1993). These remains include Boyd's Shearwater *Puffinus boydi*, White-faced Storm Petrel *Pelagodroma marina*, Cape Verde Shearwater *Calonectris edwardsii*, Brown Booby *Sula leucogaster*, and Magnificent Frigatebird *Fregata magnificens* (Boessneckt & Kinzelbach, 1993).

Over the past five centuries, the native wildlife of the Cabo Verde archipelago, including seabirds, has experienced significant declines and some extinctions (Hazevoet, 1995). Currently, Cabo Verde is home to eight species of breeding seabirds, with three of them being endemic (Hazevoet, 2001; Semedo et al., 2020), although their current distribution and abundance are influenced by a combination of factors, including various threats and specific habitat characteristics. Human exploitation of these seabird populations for centuries has led to drastic declines. Most of the remaining colonies are now located in remote and inaccessible areas, indicating that the present seabird populations in Cabo Verde are likely remnants of much larger and diverse populations in the past (Hazevoet, 2001; Semedo et al., 2020).

1.3.3. THE ISLAND OF SANTA LUZIA

The island of Santa Luzia, situated in the northern part of the Cabo Verde archipelago, contains extensive dunes with partially buried, unidentified seabird subfossils, suggesting the presence of a once-important seabird colony, presumably of White-faced Storm Petrel *Pelagodroma marina* (Mateo, 2012). No seabird extinctions have been documented on the island.

Santa Luzia, although uninhabited in the present day, has seen human activity since the early fifteenth century and remained sparsely populated until the second half of the nineteenth century (Costa, 1939; Mateo, 2012). With colonization attempts came the introduction of alien mammals to Santa Luzia, including dogs *Canis familiaris*, goats *Capra hircus*, domestic cats *Felis catus*, and house mice *Mus musculus*, likely brought to the island by the first herdsmen who settled there during the eighteenth century. Until the mid-1960s, Santa Luzia was occasionally inhabited by shepherds and goat herders and received occasional visits from fishermen from neighboring islands (Bebiano, 1932; Diniz & Matos, 1994). Currently, only one species of seabird, the Cape Verde Storm Petrel *Hydrobates jabejabe*, is found on the island (Olivera et al., 2013).

1.4. ARTIFICIAL NESTS

The choice of an appropriate nesting site is a crucial factor influencing the breeding success of most bird species. A suitable nest site helps minimize the negative impacts of predation, adverse weather conditions, and conflicts with other birds, ultimately enhancing the survival of eggs and nestlings throughout the breeding season. This, in turn, contributes to the overall breeding success and productivity of the bird population (Partridge, 1978).

For more than five decades, ornithologists have been employing artificial nests, greatly contributing to bird conservation and enriching our understanding of the ecological behaviours of birds that depend on cavities and burrows for their breeding and shelter needs. Providing artificial nests is a widely used management strategy for monitoring and conserving various bird species, including seabirds, waterfowl, passerines, parrots, and raptors (Bolton et al., 2004; Corrigan et al., 2011). These artificial nests have improved our ability to conduct field research, comparisons, and experiments as they provide easier access to nesting cavities and allow the regular monitoring and experimental manipulation of eggs or nestlings, as well as the repeated capture, identification, and handling of breeding birds (e.g., Both et al., 2004; Exo, 1992; Griffith et al., 2008; Sanz, 1998; Smallwood et al., 2009; Tella et al., 2000). Using artificial nests as research tools can also help control certain environmental factors, increasing sample sizes for scientific research. However, there are concerns regarding the generalizability of studies involving birds nesting in artificial nests, as they may differ from those in natural nest sites (Koenig et al., 1992; Møller, 1989, 1992).

Research has indicated that birds using artificial nests tend to experience higher breeding success compared to those using natural sites, primarily because of the protection they offer against predators (Møller, 1989), reduced egg damage, and fewer inter- or intraspecific conflicts (Bolton et al., 2004). Artificial nests have also been found to improve recruitment (Lalas et al., 1999), although their impact on survival remains uncertain. Artificial nests can also enhance survival by shielding individuals from predators (De León & Mínguez, 2003). However, it's worth noting that this method can also have unintended and undesirable effects, effectively serving as 'ecological traps' (Klein et al., 2007; Mänd et al., 2005). They may lead to overly dense breeding populations or even attract more predators (Mänd et al. 2005; Sanz et al., 2003).

Artificial nest structures have also been effectively utilized in the research and management of numerous burrow-nesting seabird species. For instance, they have played a crucial role in the study and conservation efforts for Procellariiform species such as the Bermuda Petrel *Pterodroma cahow* (Wingate, 1985), Wedge-tailed Shearwaters *Puffinus pacificus* (Byrd, 1979), Madeiran Storm Petrel *Hydrobates castro* (Bolton et al., 2004), and Gould’s petrel *Pterodroma leucoptera leucoptera* (Priddel et al., 2006). However, the full potential of artificial nests for conservation and research purposes remains mainly unexploited for most Procellariiform species.

1.4.1. A TOOL FOR MONITORING BEHAVIOUR IN STORM PETRELS

Monitoring behaviour of storm petrels involves various methods, some of which can be invasive, potentially disturbing the nest and affecting the birds' breeding success (Fischer et al., 2018). Non-invasive techniques may not be suitable for long-term studies on small seabirds (Fischer et al., 2017). Invasive methods like burrow-scopes or manually inspecting nest contents can be effective but may also cause disturbance and habitat damage (Parker & Rexer-Huber, 2016). Altering nest access can further impact the burrow's suitability and increase risks to the birds and their nesting environment.

The availability of suitable nesting cavities can limit burrow-nesting seabird populations (Bolton et al., 2004). Moreover, habitat modification and increased clutch predation can also limit suitable breeding locations. To address this, providing nest boxes or artificial burrows has become a common procedure, as a potential solution to mitigate these impacts and a management tool for monitoring and conserving burrow-nesting seabirds (Bedolla-Guzmán et al., 2016; Bolton et al., 2004; Bourgeois et al., 2015).

Seabird breeding success in nest boxes is generally higher than in natural sites due to better protection from predators and reduced egg damage and interference (Bolton et al., 2004; Libois et al., 2012). However, nest boxes can also have negative effects, acting as ecological traps by increasing predator attraction, reducing breeding success, and impacting fledgling survival (Klein et al., 2007; Mänd et al. 2005; Sanz et al., 2003).

Artificial nests have been used for a small number of storm petrel species (e.g., Bolton et al., 2004; Gummer et al., 2015; Ramos et al., 1997; Rayner et al., 2017), enabling observation of nesting activities that would otherwise be challenging. Storm petrels are particularly sensitive to disturbances, including handling at the nests, which can lead to negative impacts on reproductive success, site faithfulness, and increase the likelihood of divorce (Carey, 2009).

Gathering essential data for small procellariiform species, such as storm petrels, which usually nest in small burrows, presents significant challenges, resulting in relatively limited research on these species (Brooke, 2004; Rodríguez et al., 2019). Conducting research on storm petrels' breeding parameters and behaviour in both artificial nests and natural burrows is crucial for optimizing the installation and utilization of artificial nests for conservation purposes.

1.4. THESIS OVERVIEW

The general objective of this work was to provide further insights into the ecology and behaviour of storm petrels. To accomplish this, a significant part of this thesis has focused on collating and summarizing the available information on the foraging and breeding behaviour of storm petrels. Subsequently, it has focused on one species in particular: the White-faced Storm Petrel, a small oceanic seabird. The research involved the examination of an extinct colony of White-faced Storm Petrel while also investigating their current foraging behaviour and diet. Additionally, the research evaluated the potential of using artificial nests as a tool to study White-faced Storm Petrel during the breeding season and potentially also for long-term studies on other storm petrels. This approach aimed at bridging the existing knowledge gap on basic ecology and behaviour of storm petrels and enhance conservation efforts for these seabirds.

This thesis comprises a total of six chapters. In Chapter 2 existing information and studies on the foraging and breeding behaviour of storm petrels are summarized, encompassing the results of different research works. Chapter 3 addresses knowledge gaps in the at-sea foraging behaviour and diet of White-faced Storm Petrel, using lightweight (~ 1 g) GPS devices and molecular techniques. The Chapter 4 of this dissertation involves the characterization of an extinct seabird colony in Santa Luzia, Cabo Verde, and delves into the chronology of its decline and explores potential causes that may have led to its demise. Finally, in Chapter 5 a strategy involving the installation of artificial nests in existing breeding burrows of White-faced Storm Petrels was implemented, to evaluate the effectiveness of this method in enhancing the breeding performance of these seabirds. In the last chapter (Chapter 6) I provide a general discussion about the findings presented and the main conclusions of the thesis.

CHAPTER 2 - A REVIEW OF THE FORAGING AND BREEDING BEHAVIOUR OF STORM PETRELS

Storm petrels, despite having a vast geographical range, have remained relatively less studied among other bird families. This limited knowledge is due to the challenges associated with researching their at-sea behaviour, habitat utilization, and pelagic ecology, primarily caused by logistical constraints in at-sea research and the limitations of tracking equipment until recently. Additionally, their small size, preference for nocturnal activity at colonies, and tendency to breed on remote islands have further contributed to a lack of understanding of their breeding behaviour. This chapter provides, for the first time, a comprehensive list of studies that have identified and summarized the foraging and breeding behaviour of storm petrels, offering valuable insights into these elusive seabirds.

CHAPTER 3 – REVEALING THE FORAGING MOVEMENTS AND DIET OF THE WHITE-FACED STORM PETREL *PELAGODROMA MARINA* IN THE NE ATLANTIC

In this chapter we describe, for the first time, the feeding ecology and at-sea distribution of breeding White-faced Storm Petrel from Selvagem Grande, using a combination of data from tracking and DNA metabarcoding techniques. We also assessed a report on the mercury levels found in chick body feathers, providing insights into the concentration of mercury in the prey obtained from foraging areas during chick rearing.

CHAPTER 4 – CHARACTERIZATION OF AN EXTINCT SEABIRD COLONY ON THE ISLAND OF SANTA LUZIA (CABO VERDE) AND ITS POTENTIAL FOR FUTURE RECOLONIZATIONS

This chapter endeavors to provide the initial comprehensive account of the existing distribution of seabird subfossil remains on Santa Luzia, including a detailed analysis of the species composition and an estimation of the probable period of extinction through radiocarbon dating. By utilizing this data, we aim to examine the potential reasons behind the extinction of these seabirds and assess the significance of undertaking restoration efforts on the island to support breeding seabird populations.

CHAPTER 5 – ARTIFICIAL NESTS AS A TOOL FOR RESEARCH ON WHITE-FACED STORM PETREL ON SELVAGEM GRANDE, NORTHEAST ATLANTIC

This chapter was focused on the challenging task of studying and sampling burrow-nesting species, particularly storm petrels. The research aimed to assess the effectiveness of using artificial nests as a tool to study White-faced Storm Petrels during their breeding season and potentially for conservation purposes. The study examined various breeding parameters and performance of White-faced Storm Petrels nesting in both manipulated natural and artificial nests across two breeding seasons. Additionally, the research discussed factors influencing these breeding parameters in artificial nests to optimize their installation and support future long-term breeding and conservation studies of small burrowing petrels.

Moreover, the GPS tracking data on White-faced Storm Petrel used in this PhD were utilized to contribute to a manuscript focusing on topics related to relative marine plastic exposure risk for petrels at a global scale, which I co-authored. The manuscript is enclosed as an appendix:

Appendix A: GLOBAL ASSESSMENT OF MARINE PLASTIC EXPOSURE RISK FOR OCEANIC BIRDS

CHAPTER 2

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A REVIEW OF THE FORAGING AND BREEDING BEHAVIOUR OF STORM PETRELS

Maria Alho

2.1. ABSTRACT

Oceanitidae (Southern storm petrels) and Hydrobatidae (Northern storm petrels) are the two main families of the diverse group of small pelagic seabirds known as storm petrels. Despite being widely distributed and present in all oceans, they have been among the less well-known bird families. Few studies have been done to investigate the at-sea behaviour, habitat utilization, and pelagic ecology of storm petrels, owing to the logistical constraints inherent in at-sea research and the limits of tracking equipment that existed until recently. Due to their small size, predominance of nocturnal activity at colonies and typically breeding in remote islands also has resulted in a poor knowledge of their breeding behaviour. My review documented and summarized, for the first time, a full list of studies identifying the foraging and breeding behaviour of storm petrels. I conclude that there are still few studies on the subject and many basic ecological questions remain unanswered for most species of storm petrels, requiring future research. The two families (Oceanitidae and Hydrobatidae) have general physical distinctions, although it there is still a need to research with rigorous methods whether and how these variations translate to differences in foraging behaviour. Diet diversity also vary considerably between storm petrel species but studies on their diet are still scarce, mainly due to methodological challenges. How storm Petrels use their sense of smell to forage at sea and interact in colonies is one of the most researched aspects of their behaviour. It is thought that the sense of smell in these birds is more developed than other Procellariiformes. Storm petrels rely highly on public information (the visual, auditory, and olfactory presence of breeding conspecifics) to choose nesting habitats. Moreover, vocalizations are used in territorial and sexual contexts by storm petrels, and the vocalizations of some species have received more attention from researchers than other breeding behaviours. Certain species also exhibit sexual segregation in their foraging behaviour. Future research efforts should be focused on understanding the basic ecology of most species of storm petrels. We also highlight the importance of high-resolution distribution and information about their behaviour at

sea, not only during the breeding period but also, year-round data. As the knowledge gaps identified here are addressed, our understanding about foraging and breeding behaviour in storm petrels will increase.

2.2. INTRODUCTION

Procellariiform seabirds spend much of their time foraging over the ocean, coming ashore only for breeding and provisioning their chicks. Their wide-ranging foraging behaviour is generally assumed to increase the probability of encountering prey that are patchy, and widely dispersed (Benhamou, 1992). Understanding how these birds search thousands of kilometers to search for prey and exploit the vast oceans has motivated many studies of foraging strategies of seabirds (e.g., Ceia & Ramos 2015; Spear et al., 2007; Weimerskirch, 2007; Woo et al., 2008; Zhang et al., 2019). Seabirds have a vast array of morphological and physiological adaptations that enable them to exploit the ocean’s food resources in different ways. The extent and shape of foraging trips differ according to species and to oceanic habitats, as species differ in their physical characteristics and foraging strategy. There is still a lack of knowledge of the movements, behaviour and interactions among foraging adaptations (e.g., flight behaviour) of pelagic seabirds.

Past studies on the at-sea distribution of seabirds were usually carried-out by ship surveys, providing a fundamental basis for our understanding of the basic foraging ecology of many species. The spatial distribution and movement patterns of many large- and medium-sized seabird species at sea have recently been revealed by bird-borne tracking devices (BirdLife, 2020; Yoda, 2019). However, to date few studies have been conducted to describe the at-sea behaviour, habitat use and pelagic ecology of storm petrels, largely due to their small size and cryptic behaviour at sea and even at the colonies. However, continued miniaturization of tracking devices is now allowing to study many aspects of the foraging behaviour of smaller species, such as the storm petrels, that were formerly difficult or impossible to observe (e.g., Hedd et al., 2018; Rotger et al., 2020; Bolton, 2021; Alho et al., 2022).

Storm petrels are a diverse group of small pelagic seabirds and are distributed throughout the world’s oceans (Brooke, 2004a), with 27 described species (6 genera) from two main families, Oceanitidae (Southern storm petrels) and Hydrobatidae (Northern storm petrels) (Harrison et al., 2021). Although both families are found in all oceans, Hydrobatids breed mainly in northern seas, whereas Oceanitidae petrels' nest mostly in southern oceans. In spite of such a wide distribution, they have been one of the least known of avian families. The Fork-tailed Storm Petrel *Hydrobates furcatus* is an excellent illustration of this: it is the second-most abundant and widespread storm petrel, but little is known about its foraging habits outside of the breeding season.

Storm petrels breed in colonies, located generally on remote islands. Because they are highly pelagic and spending much of their time foraging at sea, information on the habits and behaviour of storm petrels has mostly been obtained during ecological studies at breeding colonies. Besides, their small size and similar colorations, particularly among Hydrobatidae (Ainley, 2005; Crossin, 1974; Howell, 2012), limit the study of their foraging behaviour. Regardless of these difficulties, ecological segregation among species includes preferences for specific marine habitats, nest site selection among sympatric breeders, and migratory behaviour (Ainley, 2005; del Hoyo et al., 1992; Spear & Ainley, 2007).

Nevertheless, the small size of storm petrels, their predominantly nocturnal activity at colonies, and distribution in remote island habitats has resulted in a lack of knowledge of the breeding behaviour for many species (Ainley, 2005; Crossin, 1974; del Hoyo et al., 1992; Howell 2012). In addition, some storm petrels reproduce during the winter, making it difficult to access their remote nesting colonies for sampling. Indeed, breeding colonies are difficult to locate and for most species breeding ecology is unknown.

Until now some species were thought to be extinct, and only in recent years the breeding sites have been discovered, such in the case of Ringed Storm Petrel *Hydrobates hornbyi*, endemic to the Humboldt Current Region. The first breeding site was discovered in 2017 in Atacama Desert, Chile, in gypsum deposits (Barros et al., 2018). Moreover, in 2013, a new storm petrel species was described, the Pincoya Storm Petrel *Oceanites pincoyae* (Harrison et al., 2013), a species for which breeding grounds are still unknown. Another example is the New Zealand Storm Petrel *Fregetta maoriana*, which was observed at sea after 108 years of being thought to be extinct (Flood, 2003). Still, twenty years after its rediscovery, little is known about the breeding biology of this critically endangered seabird. Lastly, one of the least well-known seabirds in the world, the White-vented Storm Petrel *Oceanites gracilis*, was only known to have one breeding colony, with less than ten pairs, in Chile until recently. In 2020, Barros et al. (2020) discovered two more breeding colonies for the species in the Atacama Desert.

The majority of seabird colonies are noisy and active due to the seabirds' colonial habits, which make communication a crucial aspect of their existence (Warham, 1990). Storm petrels, like many other seabirds, evolved a variety of unique physiological and sensory adaptations in response to the selective pressures imposed by their pelagic and colonial life. Some species can use a combination of olfactory and visual cues or vocalizations to assess and recognize their breeding colonies (Schreiber & Burger, 2001).

In general, storm petrels feed mostly in offshore and pelagic waters, over or beyond the continental shelf. Storm petrels snatch or pick the prey on or just below the sea surface, although some species may make shallow plunges or surface-dives (Albores-Barajas et al., 2011; Bried, 2005; Harrison et al., 2013). Foraging techniques vary among storm petrel species, to some extent in relation to the length and shape of the wings and tail (Sausner et al., 2016). Their legs are sometimes proportionally much longer than those of other petrels, with long tarsi (Sausner et al., 2016; Warham, 1977). Many storm petrel species exhibit a distinctive and unique foraging behaviour, termed “pattering” or “sea-anchor soaring”, in which they appear to walk on the surface of the ocean (Marchant & Higgins, 1990). This behaviour is used to a varying degree among species, and the extent of use seems to be related to the general morphological differences between them (del Hoyo et al, 1992; Sausner et al., 2016).

Detailed information on diet and foraging ecology is scarce for most storm petrels, but overall, their diet consists on small crustaceans, fish and cephalopods (de Hoyo et al., 1992; Brooke, 2004b; Harrison et al., 2021). Examining the diet of these small seabird species presents distinct challenges. The emergence of molecular techniques to study trophic ecology opens promising opportunities to gather information on the diet of these small seabird species, avoiding the use of intrusive methods (Symondson, 2002). Still, the existing evidence suggests that diet diversity also vary considerably among storm petrel species. The type of prey being caught is related to the type of foraging behaviour. For example, species that preferentially forage on vertically migrating fish or crustaceans, most likely feed at night. The goal of the present chapter is to review and summarize the current state of knowledge about foraging and breeding behaviour of storm petrels, and provide some insights to guide future research.

2.3. METHODS

To identify the relevant literature on the foraging behaviour, the search terms "behaviour" and “foraging” were combined with "storm petrel" or " Hydrobatidae" and with "Oceanitidae" in Web of Science database and Google Scholar, and then used the ‘snowball’ approach, by thoroughly searching both the literature cited in these articles and the articles in which they were cited. To identify the relevant literature on the breeding behaviour, we repeated the process but with combinations of the following keyword search terms: “behaviour” and “breeding” with “storm petrel” or " Hydrobatidae" and with "Oceanitidae". In order to summarize the diet studies of each storm petrel species we also search the terms "diet" and "storm petrel," each time adding the specific epithet of each storm petrel species. No book chapters were counted for this particular search. We then screened the abstracts of each article and rejected papers that were not related to at-sea foraging and breeding behaviour, diet, habitat use and pelagic ecology of storm petrels. Additional material such as books, and book chapters already in the author's possession were also used.

We reviewed a broad array of scientific publications, published in international scientific journals and books, to collect available data on the foraging and breeding behaviour of storm petrels. Few studies focus solely on foraging or breeding behaviour, with most of the studies reviewed having another subject as the central theme of the study.

Throughout this review I summarize the different foraging and breeding behaviour of the different species of storm petrels and set research priorities to improve our knowledge on how storm petrels forage at-sea and at-colony behaviour. The literature search was conducted up to December 2022.

2.4. RESULTS / DISCUSSION

In total, we reviewed 114 research articles and 5 books that investigated the foraging (N = 77) and breeding behaviour (N = 42) in storm petrels. The foraging behaviour, breeding information and diet studies of 27 storm petrel species are summarized in Tables 2.1 – 2.3. Although the database of published studies used in this review goes back to 1990, the great majority of the studies were published after the year 2005 (i.e., 74%, Fig. 2.1).

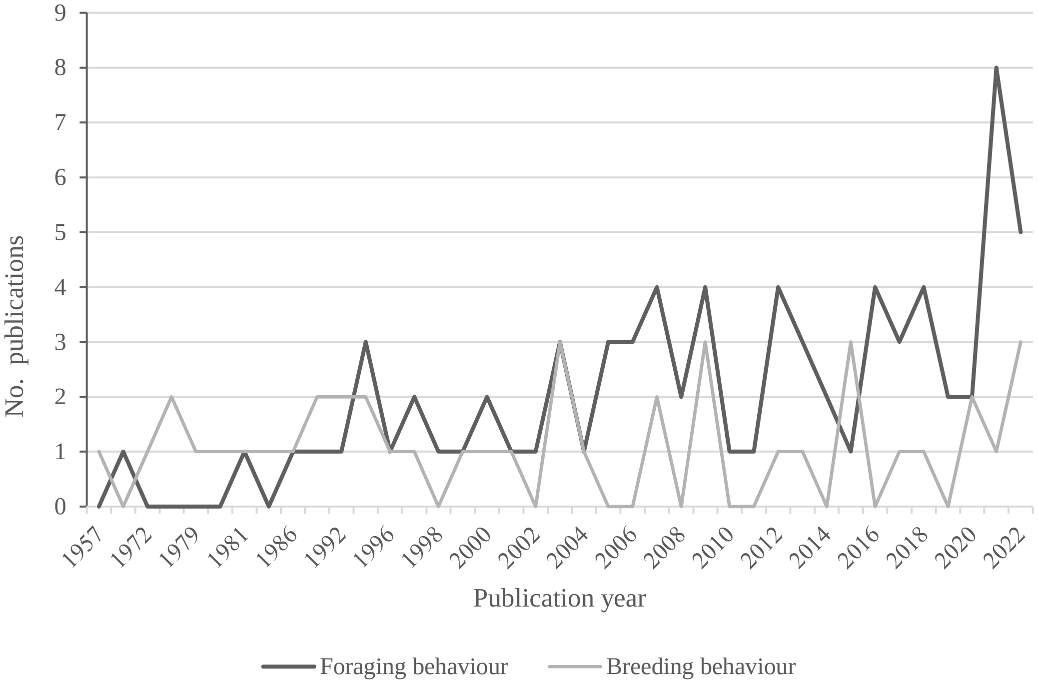

Fig. 2.1 Temporal distribution of the 119 publications analyzed in the present review

It is only since 2014 that studies of foraging movements in storm petrels using tracking devices (GLS and GPS) have started to be undertaken (Fig. 2.2). Of the 16 studies published so far, only seven species were tracked: seven studies on Leach's Storm Petrel *Hydrobates leucorhous* (Collins et al., 2022; Halpin et al., 2018; Hedd et al., 2018; Mauck et al., 2022; Pollet et al., 2014a, 2014b; Pollet et al., 2019), five on European Storm Petrel *Hydrobates pelagicus* (including three focused on the subspecies *H. pelagicus melitensis*) (Bolton, 2021; De Pascalis et al., 2021; Lago et al., 2019; Militão et al., 2022; Rotger et al., 2020), one study for Band-rumped Storm Petrel *Hydrobates castro* (Carreiro et al., 2020), White-faced Storm Petrel *Pelagodroma marina* (Alho et al., 2022), Fork-tailed Storm Petrel *Hydrobates furcatus* (Halpin et al., 2018), Monteiro's Storm Petrel *Hydrobates monteiroi* (Paiva et al., 2018) and Ainley's Storm Petrel *Hydrobates cheimomnestes* (Medrano et al., 2022).

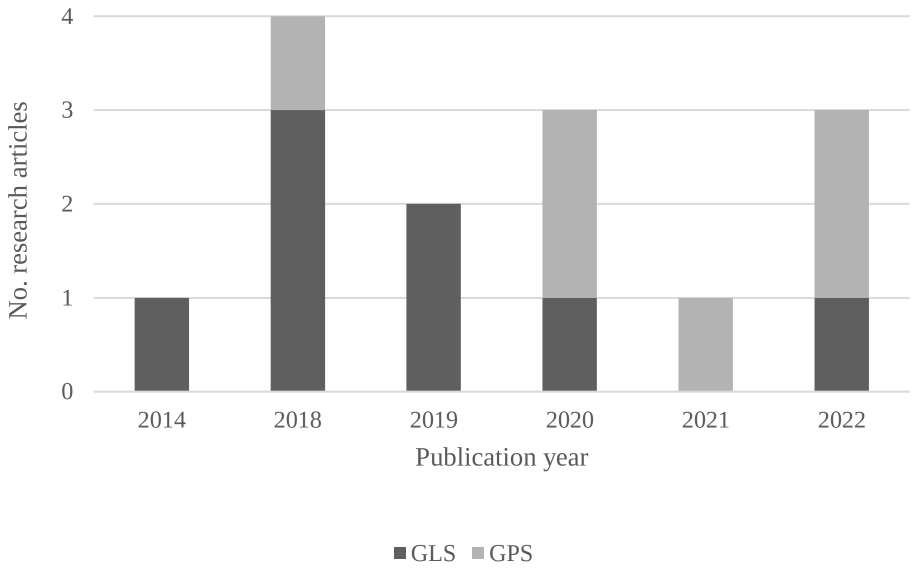

Fig. 2.2 Number of research articles on foraging movements of storm petrels using tracking devices

2.4.1 FORAGING BEHAVIOUR

General morphology

Storm petrels are the smallest and the most inconspicuous of the seabirds, with 13 to 26 cm body length and 32 to 56 cm wingspans. Therefore, the wings are much shorter relative to body length than many other petrels, especially albatrosses, gadfly petrels and shearwaters. In fact, wings are much broader and more suited for powered flight (del Hoyo et al., 1992). While general morphological differences between the two storm petrel families have been documented, including variations in flight techniques (del Hoyo et al, 1992; Harrison et al., 2021; Penhallurick & Wink, 2004; Sausner et al., 2016), it remains unclear whether and how these variances relate to differences in ecology, particularly foraging behaviour.

The Oceanitidae are generally more variable in size, shape, pattern and colour, including long legs and shorter wings as compared with Hydrobatidae. The latter group often have forked tails as an adaptation to the milder conditions of the northern seas (Harrison et al., 2021; Sausner et al., 2016; Warham, 1977). Although tail morphology in birds is known to be a source of lift and force production in flight (Thomas, 1993; Thomas & Balmford, 1995), it is still unknown how tail shape changes during flight and impacts flight aerodynamics (Evans et al., 2002). When closed, forked tails generate minimal lift but also little drag, and they are projected to be the most aerodynamically optimal tail morphology (Thomas, 1993). Certain birds that forage in open habitats rely on agility to obtain prey, and having a forked tail may be advantageous (Thomas & Balmford, 1995). This implies that there is likely a fine-scale foraging differences between species with forked tails and those without.

Even within each family there are significant morphological differences between species, which may reflect differences in foraging behaviour. Ainley et al. (1974) found that similar-sized Ashy Storm Petrel *Hydrobates homochroa* and Leach's Storm Petrel *Hydrobates leucorhous* nesting sympatrically, had significant differences in wing loadings. The author linked the low wing loading of Leach's Storm Petrel to its habit of feeding pelagically, which required less energy used per unit distance over the long distances between the colony and distant feeding areas in the ocean. Ashy Storm Petrel, on the other hand, differed by foraging on the coast and shelf break closer to the colony (Adams & Takekawa, 2008; Carter et al., 2016).

Flight behaviour

Storm petrels employ various methods to search for food, and their foraging strategies encompass a range of techniques:

1. Surface Seizing (e.g., *Hydrobates leucorhoa*, *Hydrobates castro*): This involves collecting food items using their bills while sitting on the water. It's a technique often practiced both day and night.
2. Surface Dipping (e.g., *Fregetta maoriana*, *Hydrobates castro*): When prey is spotted, these birds gradually descend and snatch prey from the water's surface, sometimes immersing their bills and even their heads.
3. Pattering (e.g., White-faced Storm Petrels *Pelagodroma marina*): Birds face into the wind with wings extended, creating a pattern on the water's surface using their feet. Given that pattering is a unique behaviour commonly observed in storm petrels, further details about this flight behaviour will be provided below.
4. Scavenging (e.g., Wilson's Storm Petrel *Oceanites oceanicus*, European Storm Petrel, *Hydrobates pelagicus*): This involves consuming carcasses of marine mammals and

seabirds, as well as other carrion, fish scraps from fishing vessels, whale blubber, whale excrement, and refuse.

5. Skimming (e.g., *Hydrobates leucorhoa*): Birds fly close to the water's surface, using their longer lower mandible to plow the water and locate concentrations of fish. This represents a successful fishing technique, particularly in areas with high prey concentrations. Skimmers may feed during the night, even in complete darkness.

It's worth noting that these techniques are not mutually exclusive. While a particular species may have a preferred foraging method, they may also occasionally utilize other techniques based on environmental conditions and food availability.

Pattering

Storm petrels are characterized by a unique foraging behaviour among seabirds, termed “pattering”, in which they appear to walk on the surface of the water and that involves the birds facing into the wind with their wings extended and pattering on the surface of the water using their feet (del Hoyo et al., 1992; Zink & Eldridge, 1980). These seabirds do not actually “walk” on the surface of the water when pattering, but, submerge their feet in the water, creating a hydrodynamic drag that counteracts the drag created by horizontal wind currents on their wings, thus using these currents to hover in place while picking prey from the sea surface (Sugimoto, 1998; Withers, 1979).

Different species use this foraging strategy to varying degrees, nonetheless the Oceanitidae family uses it more frequently (del Hoyo et al., 1992; Sausner et al. 2016). While some species, like the Leach's Storm Petrel *Hydrobates leucorhous*, are almost exclusively nonpattering, others, like the White-vented Storm Petrel *Oceanites gracilis*, almost exclusively use this foraging behaviour (del Hoyo et al., 1992).

The White-faced Storm Petrel *Pelagodroma marina*, for example, has a unique variation of pattering. It keeps its wings immobile and pushes itself off of the water with a series of bounding jumps as it faces the wind at an angle (del Hoyo et al., 1992; Harrison et al., 2021). Another example of the pattering behaviour variation is the “kick-sail” used by the *Fregetta* genus, in which it kicks off the surface of the water with one foot while foraging (del Hoyo et al., 1992; Howell, 2012). Also, the Black-bellied Storm Petrel *Fregetta tropica* was found to forage using a mix of pattering and dipping (defined as surface feeding with little or no use of the feet; Harper, 1987) (del Hoyo et al., 1992; Howell, 2012).

The Pincoya Storm Petrel *Oceanites pincoyae* also appears to differ in its mechanism of flight from the other Southern Ocean storm petrels, including *O. oceanicus* and *O. gracilis*. They fly higher (2-5 m above the sea surface) and with a direct and purposeful flight attitude than other *Oceanites spp*. and do not skip (kick off the sea surface with one foot) or skate (skate on one foot and run with feet pattering surface) like species in the genera *Fregetta* and *NesoFregetta* or bound like *Pelagodroma marina*. While pattering, it seems to use its feet more as anchors, often dipping its feet and legs completely to the middle of the tarsi, usually keeping the wings much flatter than *O. oceanicus* (Harrison et al., 2013).

Furthermore, Sausner et al. (2016) hypothesized that, in contrast to species that are almost entirely nonpattering, species that use pattering most frequently have low wing loading (mass (g)/total wing area (cm^2)), low foot loading (relative foot size mass (g)/foot area (cm^2), and a long tarsus. Given that species increase flight speed with increasing wing loading, this may explain variations in flight performance among species. For instance, compared to other *Hydrobates* species (*Hydrobates leucorhous* Collins et al., 2022; Halpin et al., 2018; Hedd et al., 2018; Mauck et al., 2018; Pollet et al., 2014a, *H. furcata* Halpin et al., 2018, *H. pelagicus* Bolton, 2021; Lago et al., 2019; Militão et al., 2022; Rotger et al., 2020), the White-bellied Storm Petrels *Fregetta grallaria* (Oceanitidae) that shows a higher wing loading is known to forage in less productive pelagic zone (Spear & Ainley, 2007), which may be an adaptation to more effectively cover a greater foraging area with faster flying speeds. While flying at sea, the White-bellied Storm Petrel also exhibits a somewhat unusual habit in that it skips off the water's surface on one leg, although the importance of this behaviour is uncertain (Howell, 2012).

Additionally, the three members of the genus *Oceanites* and White-faced Storm Petrel *Pelagodroma marina* which use pattering almost exclusively, also have yellow webbed feet (del Hoyo et al., 1992; Harrison et al., 2021). The brightly coloured webbed feet when splashing in the water may attract or frighten potential prey, making them easier for birds to detect. It is perhaps no coincidence that birds are often found with leg wounds or even without their rumps, and it seems entirely possible that these injuries were inflicted by predatory fish (del Hoyo et al., 1992; Kirkham et al., 1987; Threlfall, 1974).

Dynamic and slope soaring

Many seabirds consume a lot of energy during their movements, which is intrinsically shaped by wind fields (Weimerskirch et al., 2000), influencing their flight behaviour (i.e., the frequency of gliding, flapping, some combination of the two behaviours, and soaring (Pennycuick, 1982, 2002). Previous research has demonstrated that wind vector affects flight behaviour and that wind speed and direction affect flight speed (Spear & Ainley, 1997). To achieve and maintain flight, all flying objects require a force of lift. Most birds accomplish this by flapping their wings. However, it has been known that the albatross and other procellariiform seabirds may obtain the power of lift required to maintain or even increase height by angling themselves to the horizontal motion of the wind relative to the sea surface (Pennycuick, 2002; Spear & Ainley, 1997). This would allow them to capture kinetic energy from the air and soar without flapping their wings. Their energy consumption while flying, even in different wind speeds and directions, is nearly as minimal as when they are sitting on the nest or floating on the water (Alerstam et al., 1993; Pennycuick, 1982; Pennycuick, 2002). This common, fascinating and complicated flight maneuver is calling dynamic soaring.

Storm petrels also use dynamic soaring and slope soaring to travel and forage over the ocean surface, especially during strong winds, but to a lesser extent than the larger seabird species and within differences between species. Unlike larger seabirds that may soar at higher altitudes, storm petrels exploit the gradients of wind close to the ocean's surface, rising no more than 2 or 3 m above the sea surface for several minutes (Pennycuick, 1982). Storm petrels shelter from the wind by lingering in wave troughs where wind speeds are low, as evidenced by their reduced flight height in greater winds. Moreover, smaller storm petrels get so little energy height from gusts that it is not worth their while to rise at all, and they mainly fly by flapping (Pennycuick, 1982), and tended to fly lower with stronger winds (Ainley et al., 2015).

Dynamic soaring is used mostly by the Hydrobatidae, gaining energy from the vertical wind gradient. Conversely, Oceanitidae most commonly uses slope soaring, to slip across the ocean’s surface, turning to the wind that hits the wave fronts, gaining height (del Hoyo et al., 1992; Withers, 1979). Ainley et al. (2015) also showed that Hydrobatidae storm petrels exhibited slightly increased glides with stronger winds but Oceanitidae storm petrels did not. Leach’s Storm Petrel breeds at high latitudes but spends the winter in the tropics, whereas the other Hydrobatidae species studied are present in the same general areas all year. Thus, this difference may be related to Leach’s Storm Petrel’s longer wings. In addition, according to Power & Ainley (1986) Leach's Storm Petrel populations that nest farther from the tropics (where they wintered) have longer, thinner wings than those populations that nest closer to wintering areas, a consistent pattern with wing shape and ranging behaviour in other seabirds (Pennycuick, 1987)

Wilson's Storm Petrel (Oceanitidae) flight behaviour was characterized by Withers (1979) as a dip and rise flight with the undulations of the waves, and probable slope soaring off the wave surfaces. Since this storm petrel species has a very low wing loading making flying in strong wind conditions problematic, the birds seek cover in the wave troughs, where the wind is calmer. Wilson's Storm Petrel appear to feed by slope-soaring a few inches above the windward wave slopes in the strongest winds (Roberts, 1940). Because the metabolic cost of gliding is far lower than the cost of flapping flight, looking for food while being blown passively across the ocean surface could be an appropriate foraging technique for Wilson's Storm Petrel (Withers, 1979). When the bird needs to be stationary to pick up a food item, it can either paddle its feet or change its wing posture and enter a typical glide, remaining immobile and automatically dropping onto the food item.

Diving

Storm petrels are considered almost exclusively surface feeders. In addition to pattering, other foraging behaviours have been observed, including shallow dives (Albores- Barajas et al., 2011; Bried, 2005; Harrison et al., 2013), normally involving plunging directly from the air, quickly reappearing, and immediately taking off again (del Hoyo et al., 1992).

However, past at-sea observations have shown that some species occasionally dive: European Storm Petrel *Hydrobates pelagicus*, Band-rumped Storm Petrel *Hydrobates castro,* Black Storm Petrel *Hydrobates melania,* Fork-tailed Storm Petrel *Hydrobates furcatus*, Pincoya Storm Petrel *Oceanites pincoyae* and Wilson's Storm Petrel *Oceanites oceanicus,* Polynesian Storm Petrel *NesoFregetta fuliginosa* (del Hoyo et al., 1992; Flood et al., 2009; Flood & Thomas, 2007; Griffiths, 1981; Harrison et al., 2013, Harrison et al., 2021; Prince & Morgan, 1987; Warham, 1990). This behaviour was thought to play only a minor role in their foraging strategy (Prince & Morgan, 1987; Warham, 1990), and accurate estimates of their diving performance are still lacking. Bried (2005) studied the diving behaviour in Storm petrels for the first time, more specifically in Band-rumped Storm Petrel *Hydrobates castro* from the Azores, during the chick rearing period, using capillary tubes. They found that the average maximum dive depth was 0.85±0.33 m (range: 0.35-1.75 m, N = 16) and that such diving, essentially in the first meter of the water column, was part of its typical feeding behaviour, since all of the individuals studied dived. Nonetheless, the Madeiran Storm Petrel's capacity for diving is still severely constrained due to its poor diving adaptations, including its unstreamlined tarsi and low wing loading (Warham 1996). Additionally, Albores-Barajas et al. (2011) found that European Storm Petrels *Hydrobates pelagicus* (ssp. *melitensis*), a species thought to feed mainly on the surface (D’Elbee & Hemery, 1998), also dives for its prey, reaching up to 5 m in depth (mean: 146±0.25 cm, N = 33). Albores-Barajas et al. (2011), similarly to Bried (2005), attached capillary tubes on rump or tail feathers in order to determine the diving depth using the general gas compression formula (Mougin & Mougin, 2000).

Olfactory-mediated foraging at sea

Procellariiform seabirds are known for their large olfactory bulbs and exceptional sense of smell, with the role of olfaction particularly well studied (Bonadonna & Mardon, 2013). Storm petrels, despite their small size, also have long tubular external nostrils, associated with an extraordinary development of the olfactory part of the brain (del Hoyo et al., 1992). Many species use olfactory cues to locate both productive areas for foraging (Nevitt, 2000) and individual prey or prey-groups during area-restricted search of productive waters (Nevitt, 1999, 2000; Nevitt et al., 1995, 2004; Nevitt & Bonadonna, 2005).

Dimethyl sulfide (DMS) is a catabolic breakdown product in marine phytoplankton and is often released when zooplankton attack phytoplankton blooms (Dacey & Wakeham, 1986; Hill & Dacey, 2006). DMS is a predictor of krill grazing and it has been shown to function as a foraging cue for various storm petrel species (Nevitt, 2011), as the majority of storm petrel’s diets are composed predominantly of crustaceans, including krill, amphipods, and copepods. Nevit & Bonadonna (2005) showed that some storm petrel species can detect DMS at picomolar concentrations, and experimental evidence suggests that they are responsive to DMS deployed at sea (Humphries et al., 2012; Nevitt et al., 1995; Nevitt & Haberman, 2003).

Behavioural experiments performed ashore demonstrated that whole krill homogenates attract Leach’s Storm Petrel (Clark & Shah, 1992), providing quantitative support that krill-derived odours might serve as an olfactory cue to storm petrels foraging at sea (Nevitt & Haberman, 2003). Earliest studies suggested that Fork-tailed Storm Petrels *Hydrobates furcatus* and Leach’s Storm Petrels *H. leucorhous*, that feed on euphausiids and other planktonic organisms, use DMS to find productive areas (Nevitt 1999; Nevitt et al., 1995). Humphries et al. (2012) was also able to confirm a link between the two species and DMS concentrations at sea, creating pelagic distribution models for both species in the North Pacific. In a more recent study, Sin et al. (2019) conducted research on the olfactory receptor subgenome of the Leach's Storm Petrel, reaffirming that this storm petrel exhibits extraordinary olfactory abilities, exceeding those of the majority of waterbirds and birds in general. Nevitt et al. (1995) also demonstrated that both Wilson’s Storm Petrel and Black-bellied Storm Petrel are strongly attracted to dimethyl sulphide odour associated with krill swarms.

Small and cryptic species that nest in burrows, like storm petrels, tend to be more sensitive to DMS than other Procellariiformes and rapidly forage new or small patches of prey (Nevitt 1999; Nevitt et al., 1995). According to Nevitt et al. (2004), species that regularly forage in large, mixed-species feeding aggregations use odors associated with macerated krill to detect these aggregations from beyond the visual foraging range. This explanation is based on foraging behaviour rather than diet. Seabird species that are not as attracted to DMS tend to be larger and more aggressive, and appear to be better adapted to using several cues that include scents of crushed prey and visual cues associated with feeding by other seabirds and other marine predators (Nevitt, 1999; Nevitt & Bonadonna, 2005; Nevitt et al., 2004). On the other hand, smaller, less aggressive species, as storm petrels, may be better adapted to locate prey opportunistically, especially by detecting odors associated with krill or zooplankton grazing (such as DMS) (Nevitt, 1999; Nevitt et al., 1995). This may be due to the increased risk of predation by other larger petrels that make feeding aggregations (Harrison et al., 1991; Nevitt, 1999). In these aggregations, storm petrels tend to be restricted to the perimeter of flocks (Nevitt, 1999). The differences in the attraction of different storm petrel species to krill-scented odours may reflect not only dietary discrepancies but also species-specific divergence in foraging strategies (Nevitt, 1999).

Table 2.1 Summarized foraging behaviour and ecological information for all storm petrel species

Species	Pattering Behaviour	Diving	Foraging location	Flock feeding	Nocturnal feeding	Scavenging	Follow ships	Attracted to chum	Red List Category
Southern hemisphere species (Oceanitidae)									
Wilson's Storm Petrel *Oceanites oceanicus*	Most	Yes	Shelf; shallow waters	Yes	Unknown	Yes	Yes	Yes	Least Concern
White-vented Storm Petrel *Oceanites gracilis*	Most	Unknown	Slope and Shelf	Unknown	Unknown	Unknown	Yes	Yes	Data Deficient
Pincoya Storm Petrel *Oceanites pincoyae*	Intermediate	Yes	Shelf; inshore; shallow waters	Yes	Unknown	Yes	Unknown	Yes	Data Deficient
Grey-backed Storm Petrel *Garrodia nereis*	Intermediate	No	Shelf; deep waters near the shelf edge	Yes	Unknown	Unknown	Yes	Yes	Least Concern
White-faced Storm Petrel *Pelagodroma marina*	Most	No	Pelagic;deep waters, also near the shelf edge	Yes	Yes	Unknown	Yes	Yes	Least Concern
White-bellied Storm Petrel *Fregetta grallaria*	Intermediate	No	Pelagic	Yes	Yes	Yes	Yes	Yes	Least Concern
Black-bellied Storm Petrel *Fregetta tropica*	Intermediate	No	Pelagic/offshore	Unknown	Unknown	Unknown	Yes	Yes	Least Concern
New Zealand Storm Petrel *Fregetta maoriana*	Intermediate	Unknown	Pelagic	Unknown	Unknown	Unknown	Unknown	Yes	Critically Endangered
Polynesian Storm Petrel *NesoFregetta fuliginosa*	Most	Yes	Pelagic	Yes	Yes	Yes	Unknown	Unknown	Endangered
Northern hemisphere species (Hydrobatidae)									
European Storm Petrel *Hydrobates pelagicus*	Intermediate	Yes	Pelagic	Unknown	Yes	Yes	Yes	Yes	Least Concern
Cape Verde Storm Petrel *Hydrobates jabejabe*	Least	Unknown	Pelagic	Unknown	Unknown	Unknown	Unknown	Unknown	Least Concern
Band-rumped Storm Petrel *Hydrobates castro*	Least	Yes	Pelagic	Unknown	Yes	Unknown	Yes	Yes	Least Concern
Monteiro's Storm Petrel *Hydrobates monteiroi*	Unknown	Unknown	Pelagic	Unknown	Unknown	Unknown	Unknown	Unknown	Vulnerable
Matsudaira's Storm Petrel *Hydrobates matsudairae*	Least	Unknown	Pelagic	Unknown	Unknown	Unknown	Yes	Unknown	Vulnerable
Black Storm Petrel *Hydrobates melania*	Least	Yes	Slope; nearshore waters	Unknown	Unknown	Unknown	Unknown	Yes	Least Concern
Ashy Storm Petrel *Hydrobates homochroa*	Least	No	Slope and Shelf	Yes	Unknown	Unknown	Yes	Unknown	Endangered
Least Storm Petrel *Hydrobates microsoma*	Least	No	Shelf	Unknown	Unknown	Unknown	Unknown	Unknown	Least Concern

Wedge-rumped Storm Petrel ***Hydrobates tethys***	Intermediate	Unknown	Shelf and Pelagic	Unknown	Yes	Unknown	Unknown	Unknown	Least Concern
Townsend's Storm Petrel ***Hydrobates socorroensis***	Least	Unknown	Pelagic waters beyond the continental shelf	Unknown	Unknown	Unknown	Unknown	Unknown	Endangered
Ainley's Storm Petrel ***Hydrobates cheimomnestes***	Least	Unknown	Pelagic	Unknown	Unknown	Unknown	Unknown	Unknown	Vulnerable
Leach's Storm Petrel ***Hydrobates leucorhous***	Least	No	Pelagic	Unknown	Yes	Yes	Yes	Yes	Vulnerable
Swinhoe's Storm Petrel ***Hydrobates monorhis***	Least	Unknown	Pelagic; inshore waters	Unknown	Unknown	Unknown	Unknown	Yes	Near Threatened
Guadalupe Storm Petrel ***Hydrobates macrodactylus***	Possibly extinct	No	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Critically Endangered (Possibly Extinct)
Tristram's Storm Petrel ***Hydrobates tristrami***	Least	No	Offshore forager	Unknown	Yes	Unknown	Unknown	Unknown	Least Concern
Markham's Storm Petrel ***Hydrobates markhami***	Least	Unknown	Shelf; feeds opportunistically both inshore and offshore	Unknown	Yes	Yes	Unknown	Yes	Near Threatened
Fork-tailed Storm Petrel ***Hydrobates furcatus***	Least	Yes	Shelf; foraging closer to the shore whilst breeding	Yes	Unknown	Yes	Yes	Yes	Least Concern
Ringed Storm Petrel ***Hydrobates hornbyi***	Unknown	Unknown	Shelf	Unknown	Unknown	Unknown	Unknown	Yes	Near Threatened

General diet and habitat selection

Storm petrels, as opposed to large and medium sized procellariformes which feed mostly on cephalopods and pelagic fish (e.g., Alonso et al., 2014; Ramos et al., 2015), feed mainly on planktonic crustaceans and small fish, along with squid and pelagic fish larvae. They also feed, to a lesser extent, on mollusks, medusae, fish fry, offal, ship galley waste, and oil droplets (del Hoyo et al.,1992; Brooke, 2004b; Harrison et al., 2021). Several species are known to be somewhat more specialized, for example, the Grey-backed Storm Petrel *Garrodia nereis* that feed almost solely on Cirripedia (barnacle) larvae (Hinojosa et al., 2006; Klages et al., 1995; Newman and Ross 1971).

Some species of storm petrels are quite opportunistic, consuming a wide variety of non-cephalopod invertebrates both during the day and at night, occasionally in flocks above predatory fish, and scavenging on dead cephalopods (Spear et al., 2007). Other follow ships to forage or feed in association with cetaceans or fish, especially tuna, or other seabirds, collecting the scraps of food they leave, or small fish that are led to the surface (del Hoyo et al., 1992; Brooke 2004b). For some storm petrels that captured prey that are also targeted by fisheries, it may suggest that birds might consume fishery discards, as is in the case for European Storm Petrel and Madeiran Storm Petrels (Carreiro et al., 2020; Medeiros-Mirra, 2010). The direct use of some terrestrial (insects and plant seeds; D'Elbee & Hemery, 1998) or intertidal (nocturnal beach isopods; Thomas et al., 2006) food sources by storm petrel has even been documented by some authors.

Storm petrels are frequently solitary when at sea, however some species have been described as congregating in rafts of tens of thousands of individuals (Brooke, 2004a). For example, the Ringed Storm Petrel *Hydrobates hornbyi* and Wilson's Storm Petrel, which can gather in flocks of several thousand birds in areas which are particularly rich in food (del Hoyo et al., 1992). Furthermore, in offshore ship-based surveys it is frequent to observe interactions between different seabird species groups. For instance, Camphuysen (2007), during seabird surveys off southern Africa, reported tight gatherings between Great-winged Petrel *Pterodroma macroptera* and the Leach’s storm Petrel, two seemingly unrelated species, originating from breeding grounds in the Southern and the Northern Hemispheres, respectively (Brooke, 2004a). The tendency to "huddle" in mixed flocks, numerous encounters while foraging and feeding, and frequent aerial displays (social interactions) were described. The cause for these gatherings, particularly those involving both species, is still unknown, however it is speculated that the creation of these flocks is thought to be a component of petrels' anti-predator defense against attacks from underwater. Both species that participated in these gatherings in the study mentioned earlier are completely black, making them quite noticeable to possible underwater predators such large bony fish, sharks, or marine mammals. Storm petrels in particular, are widely known for their frequent foot wounds, which can range from broken webs to missing toes and entire limbs and are typically attributed to fish predators (Harrison, 1955; Love, 1984; Threlfall, 1974). A dense group of birds may appear more spectacular or large from below than a single bird, and with many feet congregated in a limited space, the likelihood that any given member will be preyed upon by underwater predators may be decreased.

There is a lack of knowledge about what and how much storm petrels consume while at sea, or how the diet of immature birds and non-breeding birds differ from the breeding adults or chicks. This is partly due to the potentially invasive nature of traditional sampling methods (e.g., stomach flushing), which is less acceptable among scientists who increasingly seek noninvasive or remote techniques for diet sampling. Additionally, there are also significant biases often linked to sampling gut contents or regurgitations due to differential digestion of soft and hard parts. Moreover, most methods and research focus on the brief breeding season when birds are easily accessible on or near land. According to past behavioural observations, the storm petrel's diet is believed to be primarily composed of zooplankton and small fishes (del Hoyo et al., 1992). However, more specific information regarding the trophic ecology of storm petrels is now accessible due to improvements in dietary composition methods. Stable Isotopic Analysis confirmed that storm petrels mainly consume prey from lower trophic levels, however they are able to change their feeding habits and expand their trophic niche, displaying some flexibility and opportunistic behaviour (e.g., Gladbach et al., 2007). For instance, contrary to what was assumed, regurgitations analysis of Leach's Storm Petrels collected during the breeding season revealed that chicks were eating mostly mesopelagic fish (Myctophidae and Gadidae), crustaceans, and even cephalopods (Hedd & Montevecchi, 2006; Hedd et al. 2009). Moreover, the use of molecular methods to study the feeding ecology of European Storm Petrels, showed that this species has an opportunistic behaviour, feeding not only in the most abundant prey on their habitat, like fish, cephalopods, amphipods or isopods, but also on unexpected prey such as dolphins, through scavenging (Medeiros-Mirra, 2010).

Understanding the pelagic storm petrel role in ocean ecosystems and how they use space is dependent on knowledge of their at-sea behaviour. The at-sea distribution of storm petrels is indeed highly influenced by their prey distribution, quantity and availability, as it is for most seabirds in general (Depot et al., 2020; Fauchald et al., 2000; Hunt & Schneider, 1987). Storm petrels often forage in pelagic or offshore waters that are on the shelf slope or beyond the continental shelf. The White-vented Storm Petrel *Oceanites gracilis*, which is mostly an inshore feeder in Galapagos, is a rare exception (del Hoyo et al., 1992).

Based on indices of ocean productivity, Spear & Ainley (2007) demonstrated that each species of storm petrel in the eastern Pacific has preferences for particular current-systems and ocean habitats. Storm petrel diet composition segregation suggests that prey type and foraging behaviour are connected. For instance, storm petrel that feed on actively swimming prey may choose catching them on the wing while flying, spending less time in the water (e.g., high aspect ratio and wing loading). Conversely, the capacity to patter and stay in one place for an extended length of time might be advantageous for species that feed on less mobile prey (for example, planktonic organisms) (Spear et al., 2007). Combining the study of diet with knowledge of the ecology and behaviour of their prey allows researchers to deduce detailed information about the storm petrels' foraging behaviour. For example, Cheng et al. (2010) reported that White-faced Storm Petrel, White-bellied Storm Petrel and White-throated Storm Petrel *NesoFregetta fuliginosa* make directed efforts to consume sea skaters *Halobates spp* in the eastern tropical Pacific Ocean. Sea skaters are marine insects that are small, can hide well within sea foam, and can be very fast moving. The three storm petrel species previously described exhibit unusual flight and a slow foraging behaviour, with extensive “kick splashing” against the sea surface, which may incite movement in *Halobates spp*.

Nocturnal foraging behaviour is very common in storm petrels that feed on species more likely to be present at or near the surface at night (such as vertically migrating euphausiids or bioluminescent myctophid fish) (Harrison et al., 2021). Three broad patterns regarding nighttime foraging were highlighted in the past by Brooke & Prince (1991): 1. Nocturnal feeders prefer to forage offshore as opposed to inshore. 2. Compared to cool-water northern species, there is more evidence for nighttime feeding in tropical and Southern Hemisphere species. 3. Due to the fact that most squid spend the day at depth and come to the surface at night, nocturnal foraging is frequently linked to a diet of squid obtained in the open ocean. Furthermore, considering that myctophids are mesopelagic and migrate to the sea surface at night (Gjøsaeter & Kawaguchi, 1980; Watanabe et al., 1999), the presence of myctophid species in the diet of some storm petrel species may indicate these birds feed at night and possibly over seafloor features that cause upwelling, which might increase the availability of mesopelagic prey at the surface (Watanuki & Thiebot, 2018). Several studies showed that *Hydrobates* species are markedly nocturnal, more specialized in mesopelagic prey, and more likely to feed in offshore waters (Brooke & Prince, 1991; García-Godos et al. 2002; Hedd & Montevecchi, 2006; Spear et al., 2007; Warham, 1990), since mesopelagic fish are scarce or absent in the continental shelf and other shallower areas (Gjøsaeter & Kawaguchi, 1980; Nybakken, 2001; Pusch et al., 2004).

In some species of seabirds, despite the absence of major intersexual morphological differences, one sex may forage more effectively, outcompeting the other and showing different foraging niches, or even leading to sexual segregation in foraging areas. The "intersexual competition hypothesis" can explain these differences (Lewis et al., 2002; Peck & Congdon, 2006). Paiva et al. (2018) discovered for the first time in storm petrels, sexual isotopic segregation in Monteiro's Storm Petrel *Hydrobates monteiroi* during the breeding and the non-breeding periods, with females exhibiting a narrower isotopic niche when compared to males. Other recent study demonstrated that even though both sexes of Band-rumped Storm Petrel showed a similar trophic ecology during the breeding season, intersexual differences occurred during the non-breeding season, when females displayed considerably lower nitrogen isotopic ratios than males (Carreiro et al., 2020).

On the other hand, the "energetic constraint hypothesis" proposes that varied parental investments throughout the breeding phases lead to a range of energetic or nutritional needs as well as different levels of effort to self-provisioning between sexes (Elliott et al., 2010). Hedd & Montevecchi (2006) found that Leach's Storm Petrels from Newfoundland and Nova Scotia depend heavily on mesopelagic fish to raise their young, which are high in energy (Lea et al., 2002). On the other hand, their diet in the winter included a large number of crustaceans (Hedd & Montevecchi, 2006). During the chick rearing period, Wilson's Storm Petrels also modify their diet to include more energetic prey by consuming more myctophid fish and less krill (Gladbach et al., 2007; Quillfeldt, 2002).

In recent years, research studies have been increasing using tracking devices in storm petrels to study the foraging behaviour, mostly during the breeding period (e.g., Alho et al., 2021; Bolton, 2021; Hedd et al., 2018; Rotger et al., 2020). For instance, Leach's Storm petrel colonies observed by Pollet et al. (2014a) demonstrated distinct foraging locations and foraging ranges for each colony throughout the breeding season while being just 380 kilometers away. However, very few tracking studies in storm petrels have linked dietary data provided by trophic ecological studies (Alho et al., 2021; Carreiro et al., 2020).

Table 2.2 Published research papers with reference to the dietary sampling methods of storm petrels

Species	**Dietary sampling methods**	**Diet studies**
Wilson's Storm Petrel *Oceanites oceanicus*	Spontaneous regurgitation during handling; Stable isotope analysis	Croxall et al. (1988), Quillfeldt (2002), Quillfeldt et al. (2005)
White-vented Storm Petrel *Oceanites gracilis*		None
Pincoya Storm Petrel *Oceanites pincoyae*		None
Grey-backed Storm Petrel *Garrodia nereis*	Stomach sampling (dead bird)	Klages et al. (1995)
White-faced Storm Petrel *Pelagodroma marina*	Spontaneous regurgitation during handling; Stable isotope analysis; Stomach sampling (dead birds); DNA metabarcoding	Imber (1982), Young (2013), Spear et al. (2007), Alho et al. (2022)
White-bellied Storm Petrel *Fregetta grallaria*	Stomach sampling (dead birds)	Spear et al. (2007)
Black-bellied Storm Petrel *Fregetta tropica*		None
New Zealand Storm Petrel *Fregetta maoriana*		None
Polynesian Storm Petrel *NesoFregetta fuliginosa*	Stomach sampling (dead birds)	Spear et al. (2007)
European Storm Petrel *Hydrobates pelagicus*	Spontaneous regurgitation during handling	D'Elbee et al. (1998), Thomas et al. (2006), Albores-Barajas et al. (2011)
Cape Verde Storm Petrel *Hydrobates jabejabe*		None
Band-rumped Storm Petrel *Hydrobates castro*	Spontaneous regurgitation during handling; Stable isotope analysis; DNA metabarcoding	Monteiro et al. (1996b), Carreiro et al. (2020), Carreiro et al. (2022)
Monteiro's Storm Petrel *Hydrobates monteiroi*	DNA metabarcoding	Carreiro et al. (2022)
Matsudaira's Storm Petrel *Hydrobates matsudairae*		None
Black Storm Petrel *Hydrobates melania*	Stable isotope analysis	Bedolla-Guzmán et al. (2021)
Ashy Storm Petrel *Hydrobates homochroa*		None
Least Storm Petrel *Hydrobates microsoma*	Spontaneous regurgitation during handling; Stable isotope analysis	Bedolla-Guzmán et al. (2017), Bedolla-Guzmán et al. (2021)
Wedge-rumped Storm Petrel *Hydrobates tethys*	Stomach sampling (dead birds)	Spear et al. (2007)
Townsend’s Storm Petrel *Hydrobates socorroensis*		None
Ainley’s Storm Petrel *Hydrobates cheimomnestes*		None
Leach’s Storm Petrel *Hydrobates leucorhous*	Spontaneous regurgitation during handling; Stomach sampling (dead birds); Stable isotope analysis	Hedd & Montevecchi (2006), Hedd et al. (2009), Spear et al. (2007), Frith et al. (2020), Bedolla-Guzmán et al. (2021)
Swinhoe's Storm Petrel *Hydrobates monorhis*		None
Guadalupe Storm Petrel *Hydrobates macrodactylus*		None
Tristram's Storm Petrel *Hydrobates tristrami*	Spontaneous regurgitation during handling; Stable isotope analysis; Stomach sampling (dead birds)	Harrison et al. (1983), Bond et al. (2010), Youngren et al. (2018)
Markham's Storm Petrel *Hydrobates markhami*	Stomach sampling (dead birds)	García-Godos et al. (2002), Spear et al. 2007
Fork-tailed Storm Petrel *Hydrobates furcatus*	Spontaneous regurgitation during handling	Vermeer & Devito (1988), Drummond and Leonard (2009)
Ringed Storm Petrel *Hydrobates hornbyi*		None

Migratory behaviour

In the Hydrobatidae family, following breeding season, it is known that certain species migrate great distances, as in the case of Swinhoe's Storm Petrel *Hydrobates monorhis* which breeds in the west Pacific and migrates to the west Indian Ocean. Some travel shorter distances, like in the case of the Black Storm Petrel *Hydrobates melania* which breeds in southern California and migrates down the coast of Central America as far south as Colombia (Harrison et al, 2021). Pollet et al. (2014b) tracked 13 individuals of Leach’s Storm Petrel breeding at two colonies in Nova Scotia and results indicated that individuals have low migratory connectivity: some birds remained in the North Atlantic, others travelled farther and overwintered off South Africa. In a recent study of the European Storm Petrels breeding on Benidorm Island, geolocators were used to reveal their migratory patterns. This study found that these birds undertake migrations to the North Atlantic Ocean, covering a range extending from the Canary Islands to the southern regions of Iceland (Militão et al., 2022). In contrast, the Mediterranean subspecies *H. p. melitensis* is primarily believed to be year-round residents of the Mediterranean basin, with only a minority of the population migrating into the Atlantic (Lago et al., 2019; Martínez et al., 2019).

Within the Oceanitidae family, Wilson's Storm Petrel, which breeds in Antarctica and the subantarctic islands, is the most widely travelled migrant, regularly travels across the equator to the northern Pacific and Atlantic Oceans. On the opposite hand, another species from the same family, the Grey-backed Storm Petrel, is thought to be fundamentally sedentary, not leaving the waters around their breeding colonies (del Hoyo et al., 1992; Harrison et al., 2021). From the limited knowledge available about White-faced Storm Petrel during the non-breeding period, previous observational studies have revealed distinct behaviours among different subspecies of the White-faced Storm Petrel. Those breeding in the northern hemisphere tend not to engage in full migration but rather disperse from their breeding areas during the winter months (Montalti & Orgeira, 1997; Warham, 1990). On the other hand, the Australian subspecies, *P. marina dulciae*, exhibits a comprehensive trans-equatorial migration pattern. Western Australian populations have been observed wintering in the northern Indian Ocean and Arabian Sea, while the migratory route of the southeastern Australian populations remains uncertain (Serventy et al., 1971; Warham, 1990). Potential migration routes for these southeastern populations include traveling westward toward the Indian Ocean or heading north-northeast into the tropical Pacific (Imber, 1981).

2.4.2. BREEDING BEHAVIOUR

Nesting sites

Notwithstanding the fact that studying the behaviour of storm petrels has been centered on breeding colonies, there are still several limitations on this field of research. Regarding the Oceanitidae family, for instance, there is a lack of understanding about where White-vented Storm Petrel and Pincoya Storm Petrel breed and their population trends and threats, resulting in the only two species of storm petrels classified as Data Deficient on the IUCN Red List (BirdLife International, 2022a,2022b). Storm petrels typically breed in colonies on islands, with few species breeding on the mainland (e.g., Ringed Storm Petrel *Hydrobates hornbyi* breeding in the Atacama Desert, Chile; Barros et al., 2018; Medrano et al., 2019). Their numbers can be as high as 1.95 million breeding pairs in Leach's Storm Petrel *Hydrobates leucorhous* colonies (Wilhelm et al., 2019) or 840.000 breeding pairs, in the case of White-faced Storm Petrel *Pelagodroma marina* nesting in the Chatham Islands, with burrow densities of between 1.18 – 0.47 burrows/m² (West & Nilsson, 1994). In contrast, Tristram’s Storm Petrel *Hydrobates tristrami* breeding in Laysan (Northwest Hawaiian Island) was estimated to be only 700 breeding pairs.

Storm petrels specialize in using small nest cavities, where they may achieve a high level of protection (Ramos et al., 1997). The majority of species typically nest in rock crevices or burrows, though some species dig their own nesting burrows (e.g., White-faced Storm Petrel) or occupying abandoned ones (e.g., European Storm Petrel) (del Hoyo et al., 1992). Additionally, the Ringed Storm Petrel *Hydrobates hornbyi* nests in cavities in gypsum outcrops and in saltpeter cavities (Barros et al., 2018; Medrano et al., 2019) and the Markham’s Storm Petrel *Hydrobates markhami* which also nests in saltpeter crevices (Barros et al., 2019; Schmitt et al., 2015; Torres-Mura & Lemus, 2013), both breeding in desert of northern Chile. Moreover, the Grey-backed Storm Petrel *Garrodia nereis* nests in cavities formed at the base of dense vegetation instead of burrows or rock crevices (Carrick & Ingham, 1967).

Artificial nests, which are mostly used as a research tool, are also occupied by several species of storm petrels (*Hydrobates leucorhous* Buxton & Jones 2012; Podolsky & Kress, 1989 , *Hydrobates pelagicus* Bolton, 1996; De León et al., 2003; Dell'Ariccia et al., 2015; Libois et al., 2012; Mariné & Bernard, 2020, *Hydrobates castro* Allan, 1962; Bolton et al., 2004, *Hydrobates furcatus* Buxton & Jones, 2012, *Pelagodroma marina* Rayner et al., 2017), suggesting that natural burrows may be a limiting factor in some colonies or/and some species are not very strict or demanding in terms of conditions for burrowing.

According to Forbes & Kaiser (1994) and Warham (1990), burrowing Procellariiformes have a strong sense of colony and nest site persistence, and competition for nest cavities can occur both within and between species. The smaller species, like storm petrels, in mixed-species colonies of cavity-nesting Procellariiformes are likely to be at a significant competitive disadvantage in conflicts over nest ownership. A previous study has shown that competition for nest sites exists among Madeiran Storm Petrels *Hydrobates castro* and the smaller procellariiform species in the Azores islands (Ramos et al., 1997).

Attendance at the breeding colonies

In addition to nesting in burrows, storm petrels typically attend colonies at night (Marchant & Higgins, 1990; McNeil et al., 1993; Warham, 1996), in order to avoid predation pressures (Brooke & Prince, 1991; McNeil et al., 1993). It has commonly been assumed that the nocturnal activity of storm petrels is related with the potential risk of birds being attacked (Brooke & Prince, 1991; McNeil et al., 1993), since they are particularly vulnerable to aerial predators when they are close to land (McNeil et al., 1993). The Wedge-rumped Storm Petrel is the only storm petrel to arrive on land during the day during the breeding season. This deviation is still unaccounted for because the Short-eared Owl *Asio flammeus*, is the primary predator of this species, hunting during the day and the night on the Galapagos Islands.

However, skuas and gulls have been observed hunting at night as well (McNeil et al., 1993; Watanuki, 1986; Phillips et al., 1996, 1997; Mougeot et al., 1998; Mougeot & Bretagnolle 2000; Votier et al., 2006), although their predation efficiency during nighttime is likely lower than during daylight hours due to the challenges of locating and chasing prey in the dark. Previous research demonstrated that non-breeding storm petrels at colonies are more vulnerable to nighttime predation than breeding individuals since they spend more time out of burrows looking for a mate and a potential breeding site (Adam & Booth, 1999; Huntington et al., 1996; Morse & Buccheister, 1977; Votier et al., 2006). Nevertheless, Oro et al. (2005) estimated that at least 11–14% of Leach’s Storm Petrel killed by gulls at Benidorm Island (western Mediterranean) during 1993–2003 were breeders.

In storm petrels that breed in high latitudes with relatively long summer nights, nocturnal activity patterns are well described. Bright moonlight has been shown to reduce nighttime activity at the colonies (e.g., less vocally) (Mougeot & Bretagnolle, 2000; Watanuki, 1986; Warham, 1990). For example, Fork-tailed Storm Petrel (Boersma et al., 1980; Harris 1974), and Leach's Storm Petrel (Harris, 1974; Watanuki, 1986) are both strictly nocturnal in their colonies and less active on moonlit nights than on dark nights. Studies of nocturnal activity patterns in storm petrels that breed at high latitudes (e.g., Simons, 1981 for Fork tailed Storm Petrels; Bretagnolle, 1988 for Wilson's Storm Petrels) are scarce. Around the summer solstice, these regions exhibit extremely brief, bright nights with high light levels, followed by rapidly lengthening nights as the season progresses. Species found at high latitudes delay the onset of their breeding season by several weeks and primarily visit their nests during the periods of the day with the lowest light levels (del Hoyo et al., 1992). In some colonies of storm petrels in the Artic, where daylight is continuous during the summer, the Black-bellied Storm Petrel is preyed by diurnal Great Skua *Catharacta skua* and still show nocturnal activity (Beck & Brown, 1971). In Japan, Leach’s Storm Petrel are also killed by diurnal gulls and exhibit nocturnal activity as well as moonlight avoidance behaviour (Harris, 1974; Watanuki, 1986).

Coursthip stage and vocalizations

Aerial and ground activity/Nuptial display

The nocturnal flights over the breeding colonies by some species of storm petrels are notable. Some species engage in aerial pursuits as part of their nuptial display, which involves flying quickly in circles above the nesting area while one bird closely follows the other and both calling repeatedly and loudly (del Hoyo et al., 1992; Harrison et al., 2021; Warham, 1996). The noticeable rump patch on some species may be particularly useful in this exercise, which is carried out quickly and in almost complete darkness. One or both of the birds will eventually land to locate, inspect, and occupy a nest site (del Hoyo et al., 1992; Warham, 1996). Breeders can reduce the risk of predation by flying directly into the nest chamber, in complete darkness, often with numerous other birds fluttering around in the same area (del Hoyo et al., 1992). However, the Wedge-rumped Storm Petrels fly silently around the colony during the day, occasionally descending to patter on the ground. It is not known if they are prospecting nests, mates or both (del Hoyo et al., 1992; Schreiber & Burger, 2001).

Coordinated aerial activity is known for European Storm Petrel (Davis, 1957), Band-rumped Storm Petrel (Allan, 1962; Harris, 1969), Leach's Storm Petrel (Ainslie & Atkinson, 1937; Waters, 1964), Fork-tailed Storm Petrel (Simons, 1981), Wedge-rumped Storm Petrel (Harris, 1969), Black-bellied Storm Petrel (Beck & Brown, 1971), Wilson's Storm Petrel (Roberts, 1940) and Markham's Storm Petrel (Torres-Mura & Lemus, 2013). There is a lack of knowledge regarding other storm petrel species and how much of the flighting is just the normal circling before landing or has any nuptial display content.

Leach's Storm Petrels engage in nuptial behaviours above and after landing in the colony (almost certainly pre-breeders' birds) and are apparently at a far greater predation risk from predators such as skuas than those that disappear quickly to their burrows (most likely breeding birds) (Harris, 1974, Schreiber & Burger, 2001). This is supported by behavioural studies of both breeding and non-breeding petrels regarding aerial activity (Bretagnolle, 1990; McNeil et al., 1993; Storey, 1984; Watanuki, 1986), indicating that the aerial display activities have likely significant social significance, particularly among pre-breeders (Schreiber & Burger, 2001).

In storm petrels, no sexual behaviour has been observed at sea. Storm petrels do not have a "honeymoon period" when both partners are out at sea gaining weight in anticipation of the upcoming task, like the majority of other members of the Procellariiformes order do. Actually, the nest cavity is where the couple engages in the majority of their sexual activity. According to the scant information available, copulation typically occurs inside the burrow or on the ground (del Hoyo et al., 1992; Warham, 1996). In the burrows, some species could spend hours calling, touching bills, and preening each other. As is the case with many other petrel species, partners sing incessant duets in the nest hole in some species, like the Leach's Storm Petrel (del Hoyo et al., 1992).

Vocalizations

In Procellariiform species that build their nests in burrows, as is the case for most storm petrel species, vocalizations are used in territorial and sexual contexts. It is known that storm petrels base their decision to select nesting habitat on information, such as conspecific vocalizations (James & Robertson, 1985; Taoka et al., 1989a; Warham 1990, 1996). Voice distinguishes sympatrically nesting species, and the vocalizations of storm petrels may vary depending on the gender, appearing to be important for intraspecific communication. The repertoire normally consists of a burrow call, a flight call, a variety of strong agonistic sounds, and high-pitched distress calls. However, the majority of the storm petrels' aerial calling's purpose is still largely unknown (Warham, 1990, 1996; Schreiber & Burger, 2001).

One of the most studied topics in breeding behaviour is the analysis of vocalizations in storm petrels, as for the following species: European Storm Petrel (James, 1984a), Band-rumped Storm Petrel (James & Robertson, 1985), Wilson's Storm Petrel (Bretagnolle 1989; Bretagnolle & Robisson, 1991), Tristram's Storm Petrel (Marks & Leasure, 1992) and on Leach's Storm Petrel and Swinhoe's Storm Petrel (Taoka et al., 1988, 1989b; Taoka & Okumura, 1988, 1989, 1990). In addition, more recently, Markham's Storm Petrel has been observed flying in circles above the nesting area, vocalizing frequently during nuptial displays in the desert of northern Chile. Moreover, birds also called in flight and from within their burrows (Torres-Mura & Lemus, 2013).

Based on the currently available data on vocalizations, there appear to be no behavioural features that distinguish the Hydrobatidae from the Oceanitidae family, despite the fact that the former appears to call more in flight than the latter (Warham, 1996). Moreover, most northern species produce whirring, churring, or creaking sounds based on very brief pulses, while the southern species use rather high-pitched twitters or whistles like or quite harsh repeated calls primarily of "noise," as with *Oceanites oceanicus* and Grey-backed Storm Petrel *Garrodia nereis*.

Petrels are nocturnal in their nesting areas and avoid moonlit nights due to the risk of predation (Bretagnolle, 1990; McNeil et al., 1993; Watanuki, 1986). While not certain for all storm petrel species, a hypothesis suggests that aerial calling is a behaviour exhibited by some species as a means of conducting part of their mating process in flight, which serves to further reduce the risk of predation. Nonetheless, it is possible that species that experience substantial predation will employ signals whose physical structure, which includes the presence of a noise component and their use of fewer syllables, may be defense mechanisms against predators, making them even harder for predators to detect (Bretagnolle, 1996). Additionally, species that belong to the same genus vary substantially regarding the presence or absence of aerial calling.

Some species may not have aerial calling because of predation pressure. However, species with and without aerial calls frequently breed nearby (Bretagnolle, 1996). For instance, on Selvagem Grande island (Madeira, Portugal), White-faced Storm Petrel give no aerial calls (James, 1984b), whereas the Band-rumped Storm Petrel do and both are vulnerable to predation by gulls.

Hahn (2000) studied the behavioural patterns of the Black-bellied Storm Petrel *Fregetta tropica* during the breeding season in the King George Island, Antarctica. As is typical for many nocturnal species, the main periods of colony activity were closer to dark than to dawn (Brooke & Prince, 1991; Hahn, 2000). The main calling activity was only triggered by the moment of sunset, whereas sunrise and sunset determined the maximum amount of time for flight (Taoka et al., 1989b). Based on the constant threat of skua predation (Hahn & Quillfeldt, 1998), behavioural patterns, and particularly vocal behaviour of *Fregetta tropica*, shifted with the seasonal periods. There was a high amount of vocal activity during the pre-laying period (Hahn, 2000), which is thought to be due to the concentration of all activity during the brief nights and pair bonding behaviours (Beck & Brown, 1971). Unmated birds should strengthen their vocalizations for mate attraction later in the season (during the incubation period), and along with the calls of the breeders, the vocal activity reached its seasonal peak (Hahn, 2000).

Storm petrels also use vocalizations to defend their nests against other petrels (Warham, 1996). There is evidence of ground activity for the *H. furcatus* (Simons, 1981) during the pre-incubation period, with newly paired birds indulged in bouts of calling interspersed with the alternate allopreening. Also, Harris (1969) described a defensive nest behaviour in the ground by *H. Tethys*.

Sex differences in vocalizations

James & Robertson (1985) hypothesized that most Procellariiformes species with sexually dimorphic calls also engage in aerial calls, in contrast to species without such dimorphism that are silent in flight. Exceptions belong to the group of storm petrels. The European Storm Petrel *Hydrobates pelagicus*, which sporadically calls while flying but exhibits sexual dimorphism in its call (Hall-Craggs & Sellar, 1976; James 1984a). Nevertheless, the dimorphism only manifests itself in a male-only call. The Fork-tailed Storm Petrel *Hydrobates furcatus*, calls while flying but also has a call that is only made by males on the ground or in burrows (Simons, 1981). The flight call is made by both sexes and seems to be similar.

Male competition for nest sites is another possibility as to why some species lack aerial calling. If nest sites were scarce, the worth of leaving a burrow to display in flight might be losing the burrow to another prospecting male. Males may not be able to leave their burrows to perform in flight displays in some species where burrow competition is fierce. They might stay in their burrows and call to attract potential mates. In species without aerial calling, sexual dimorphism in calls may not be necessary because prospecting females would recognize males making calls from burrows as such. It has been suggested that in species where males do not call in flight, females will also remain silent. Sexual dimorphism in voice may have evolved in species where both sexes make aerial calls to aid in pair formation in the dark (James & Robertson, 1985).

Band-rumped storm petrels are quite loud at the colony, using calls to entice and keep possible mates as well as to signal burrow occupancy (James & Robertson 1985; Bretagnolle, 1996). In Atlantic breeding populations, the flight calls of Band-rumped Storm Petrels are sexually dimorphic, with males generating a clearer, more melodic call than females (James & Robertson, 1985). Smith & Friesen (2007) described minor differences between cold and hot season on male flight calls of Band-rumped Storm Petrels from the Galapagos Islands. Several call traits were very variable, implying that the characters examined may not be species-specific indicators, but rather aid in individual recognition (Bretagnolle & Lequette, 1990). Male Wilson's Storm Petrel calls vary significantly among populations as well, but certain parameters are more stable (e.g., modal frequency, duration of syllables; Bretagnolle & Robisson, 1991). Experiments with playback have shown that these stereotypic call traits (consistent and characteristic vocal calls within a species) are what attract nonbreeding females (Bretagnolle & Robisson, 1991).

Buxton & Jones (2012) demonstrated that both Leach's Storm Petrel and Fork-tailed Storm Petrel were strongly attracted to playback of conspecific calls and moderately to playback of heterospecific calls. However, when the authors combined conspecific odor and playback cues, the Fork-tailed Storm Petrels were more attracted to enter to artificial burrows than Leach’s Storm Petrel. Leach's Storm Petrel colonies frequently coexist with Fork-tailed Storm Petrel colonies over the majority of their range (Boersma et al., 1980; McChesney & Carter, 2008; Vermeer et al., 1988). Moreover, they share similar nesting habitats (Stenhouse & Montevecchi, 2000) and diet, despite some minor variances (Vermeer et al., 1988). Also, both species produce a range of loud, nocturnal vocalizations for communication (Boersma & Silva, 2001; Huntington et al., 1996). Vocal information should be helpful to both species because high-quality habitat for them is similar in terms of burrow location. To learn about breeding habitat, prospecting birds should be able to receptive to either conspecific or heterospecific storm petrels. The Leach’s Storm Petrel has a more territorial behaviour (Taoka et al., 1988), and is perhaps less likely to enter unoccupied burrows (Huntington et al., 1996) than is the Fork-tailed Storm Petrel. This suggest that Fork-tailed Storm Petrel use odor as public information while scouting for safe nesting habitat, while Leach's Storm Petrel may employ odor as an occupancy indicator (Buxton & Jones, 2012).

Begging behaviour in chicks

The vocal components of begging behaviour in Procelariiformes are important in the communication between parents and chicks, as a mean of providing information about the current nutritional status of chicks (e.g., Granadeiro et al., 2000; Harris, 1983; Henderson, 1975; Quillfeldt, 2002; Quillfeldt et al., 2004). Gladbach et al. (2009) discovered that several acoustic aspects of begging calls of Wilson’s Storm Petrel chicks carry information about their body condition, and that in some situations, parents seemed to limit the meal quantity they delivered as a result of variations in these factors. Rhythmic and lengthy sounds are the main elements in two distinct begging calls used by Wilson's Storm Petrel chicks. Extended begging calls are only made when an adult is present (Quillfeldt, 2002). Rhythmic calls are first made when an adult enters the nest, followed by a string of protracted begging calls. Higher frequency sounds are made by poorer condition chicks, and these higher pitched calls also lead to the chick receiving more attention, such as larger meals (Gladbach et al., 2009).

The vocal ontogenesis in non-passerine birds remains understudied, although, the available data related to storm petrel calls suggests that the process of call development is a voice-breaking process (Marchenko & Beme, 2022). This process refers to an abrupt change to adult vocalization and occurs at a specific point in the bird's life. Despite a large rise in body weight, the chick maintains high-frequency calls for a long period. This process has been described in the Fork-tailed Storm Petrel, where the call frequency of chicks does not change during the nesting period, remaining at the level of 2–4 kHz (Naugler & Smooth, 1992). At the same time, the call frequency of adult birds is below 1 kHz (Taoka et al., 1989b).

Extra-pair fertilization and divorce

Storm petrels exhibit a high degree of philopatry by returning to their original colonies to breed. In the fourth or fifth year, storm petrels typically reach sexual maturity and exhibit extreme fidelity to their breeding grounds (Brooke, 2004a).

As all Procellariformes, storm petrels are long-lived birds characterized by long-lasting pairbonds, single-egg clutches, and extended parental care. Several studies showed no evidence of extra-pair copulations or extra-pair fertilizations, unlike many other monogamous Procellariiformes, which is not surprising considering these are burrow-nesting seabirds that lay only one egg per year and show high biparental investment (Bried et al., 2003; Mauck et al., 1995; Quillfeldt et al., 2001). Using multilocus minisatellite DNA fingerprinting, Mauck et al. (1995) estimated the frequency of extrapair fertilizations to be totally absent in a population of Leach's Storm Petrels on Kent Island, Canada.

Procellariiformes exhibit low divorce rates (e.g., 4% per annum in the Northern Fulmar *Fulmarus glacialis* Macdonald, 1977, 1-8% per annum in the Long-lived black-browed albatross *Thalassarche melanophris* Bried & Jouventin, 2002; Ventura et al., 2021). The 'incompatibility' hypothesis states that pairs with little shared breeding experience and poor reproductive performance should be most likely to divorce. Alternatively, the 'better option' hypothesis states that divorce is generally associated with a higher likelihood of successfully breeding with a new partner.

It has been proposed that fidelity rates can be used as indices of population health, with a high rate of nest changes and divorces brought on by unsuitable partners and environment (Robert et al., 2014). Individuals with high levels of mate fidelity may be in good physical shape, have well-coordinated incubation and foraging search routines, or are genetically compatible (Bourgeois et al., 2014; Bried & Jouventin, 2002). In one of the two studies addressing this topic in storm petrels, Nava et al. (2017) reported a divorce rate of 14.2% (N = 415 pair × years) between 2000 and 2012, and the longest pair bond recorded during this period for the endemic Monteiro’s Storm Petrel *Hydrobates Monteiro* in the Azores Archipelago lasted for 14 years. Furthermore, according to Mariné & Cadiou (2019), European Storm Petrels exhibited significant levels of mate and nest site fidelity throughout the study period from 2001 to 2018, with a remarkably high percentage of individuals continuing to breed at the same location (94%) and with the same partner (95%).

Egg neglect

Similar to other Procellariiformes, storm petrels only lay one egg during a breeding season, which is incubated by both sexes in shifts (del Hoyo et al., 1992). The length of the incubation period varies among species and within individuals (Table 2). For example, Wilson's Storm Petrel *Oceanites oceanicus* incubate the egg between 33 to 53 days (Beck & Brown, 1972) and White-faced Storm Petrel has incubation period between 46 to 60 days in the North-east Atlantic (Campos & Granadeiro, 1999). Part of variability in the duration of the incubation period might be due to temporary egg neglect, i.e., birds leaving the egg unattended for some days, in the absence of their partner.

Egg neglect is defined as the proportion of the incubation period that the egg was left unattended by either parent. White-faced Storm Petrel *Pelagodroma marina* (Boersma & Wheelwright, 1979; Campos & Granadeiro, 1999; Jouventin et al., 1985; Richdale, 1965; Underwood & Bunce, 2004), Wilsons' Storm Petrel *Oceanites oceanicus* (Beck & Brown, 1972; Pefaur, 1974; Roberts, 1940), Black-bellied Storm Petrel *Fregetta tropica* (Beck & Brown, 1971), European Storm Petrel *Hydrobates pelagicus* (Davis, 1957), Band-rumped Storm Petrel *Hydrobates castro* (Harris, 1969), Wedge-rumped Storm Petrel *Hydrobates tethys* (Harris, 1969) and Leach's Storm Petrel *Hydrobates leucorhous* (Wilbur, 1969) have been noted to neglect their eggs for periods ranging from a few hours to six days. Egg neglect in storm petrels can lengthen the incubation period as long as the egg is still viable at all stages of incubation, from very early on to just days before hatching (Boersma & Wheelwright, 1979; Richdale 1965; Campos & Granadeiro, 1999; Jouventin et al. 1985; Pefaur, 1974; Underwood & Bunce, 2004). Although many procellariiformes neglect their eggs, none have been found to do so to the extent of the Fork-tailed Storm Petrel *Hydrobates furcata* breeding in the Gulf of Alaska (Boersma & Wheelwright, 1979; Boersma et al., 1980). Fork-tailed Storm Petrels’ eggs are frequently neglected by parents during incubation for a few days at a time, and embryos can withstand a total of

28 days of neglect during incubation periods that can finally last more than 60 days (Boersma et al., 1980). The temperature experienced by the eggs during these periods of neglect is approximately 10ºC (Boersma & Wheelwright, 1979). Even when attended by adults, incubation temperatures (29.7ºC) are notably lower than those typically observed in other bird species. Fork-tailed Storm Petrel embryos can hatch successfully at lower temperatures compared to most other bird species, and they develop normally even at temperatures that would be detrimental for other bird species (Drent, 1975). Other storm petrel species also have eggs that can tolerate chilling during incubation (Boersma & Wheelwright, 1979; Roberts, 1940). This exceptional cold tolerance during incubation sets storm petrels apart as birds that can endure extended periods of chilling. Boersma & Wheelwright (1979) found a positive linear relationship between the length of the incubation period and egg neglect in Fork-tailed Storm Petrels. Boersma (1982) estimated that egg neglect alone was responsible for 80% of the variation in the length of the Fork-tailed Storm Petrel incubation period. Moreover, compared to nonneglected eggs, neglected eggs had lower hatching success and chicks showed higher mortality and were smaller for at least the first 20 days after hatching (Boersma & Wheelwright, 1979). In general, neglecting eggs increases the likelihood of breeding failure (Chaurand & Weimerskirch, 1994; Zangmeister et al., 2009). Granadeiro & Campos (1999) observed a period of egg neglect in White-faced Storm Petrel of one to six days and occasionally, just a day or two before hatching, eggs were neglected and still successfully hatched. Besides, the length of the incubation period in this population varied significantly, with some pairs incubated their eggs 30% longer than others due to egg neglect.

Investment in parental needs (foraging, self-maintenance) and subsequent costs for current reproduction may manifest during incubation as decreased coordination between members of the pair in species that practice biparental care. Due to a lack of coordination, the incubating parent may leave the nest before the other has returned from foraging, leading to egg neglect (Shoji et al., 2011; Zangmeister et al., 2009). Given that many storm petrel species are likely to encounter storms at sea or have variable food sources, it is possible that some of this lack of coordination is caused by these factors, which delay the mate's arrival at the nest (Boersma & Wheelwright, 1979). As a result, compared to other Procellariiformes, storm petrels have therefore acquired a higher level of embryonic tolerance to chilling. This neglect can be costly to the nestling and to the reproductive performance of the parent.

Olfactory-mediated behaviour at the colony

The olfactory sense plays an important role in social communication and recognition of storm Petrels (Buxton & Jones, 2012; Grubb, 1974). Storm Petrels, in particular, have a strong and persistent musky-smelling plumage imbued with volatile chemicals that they transmit to their burrows, an odour that may give them individual olfactory signatures (Jennings et al., 2022; Jennings & Ebeler, 2020; O'Dwyer et al., 2008). Moreover, several burrow-nesting species use olfactory cues to locate their nest when returning to the colony for the breeding season (Bonadonna et al., 2004; Bonadonna & Bretagnolle, 2002). The ability of individuals to recognize their burrow by smell has been established in several species of Petrels, including storm Petrels (Bonadonna & Bretagnolle, 2002; Grubb, 1974; Jouventin et al., 2007; Nevit & Bonadonna, 2005; O'Dwyer et al., 2008; Verheyden & Jouventin, 1994).

The first studies to investigate the role of olfactory cues in homing were mainly carried out on storm Petrels, particularly in Leach's Storm Petrel *Hydrobates leucorhous* (Grubb, 1973, 1974, 1979). These pioneer studies found that Leach's Storm Petrel consistently approached burrows from downwind, suggesting that olfactory cues guided this behaviour, and also revealed that they can smell an odour plume emanating from the substrate near their burrow and use it to detect and locate the entrance to their own burrow. This idea was confirmed in later experiments where birds were tested in Y-mazes: Leach's Storm Petrels tended to choose arms with nesting material over arms with forest floor substrate (Nevit & Bonadonna, 2005). The sense of smell also plays an important role in social communication and recognition of individuals in this species (O'Dwyer et al., 2008). Moreover, chicks can recognise and prefer familiar odour of their burrow material from other petrel odours, which may play a role in kin recognition and mate choice later in life (O'Dwyer et al., 2008). Although the link to individual odour profiles has not yet been established, mate choice by Leach’s Storm Petrel males has recently been demonstrated in this species (Hoover et al., 2018).

Wilson’s Storm Petrel *Oceanites oceanicus* use olfactory sense for nest recognition (Bonadonna & Bretagnolle, 2002) as well. In addition, Wilson’s Storm Petrel can recognize and prefer their mate’s odor to the odor of an unknown bird (Jouventin et al., 2007). This appears to be true in European Storm Petrels *Hydrobates pelagicus* too (De León et al., 2003). Additional behavioural studies also demonstrated that European Storm

Petrel's chicks could also recognize their self-odour and preferred it (De León et al., 2003; Minguez, 1997). Bonadonna & Sanz-Aguilar (2012) provided the first evidence for kin-related individual odour recognition in a wild bird species, suggesting that European Storm Petrels are able to recognize and distinguish kin from nonkin odour cues.

Foraging behaviour during the breeding period

Sexual size dimorphism within certain Procellariiformes species has been linked to segregation in foraging areas (e.g., Shaffer et al., 2001). Among Procellariiformes, both male-biased and female-biased sexual size dimorphism can be observed, although male-biased sexual size dimorphism is predominant, with males being larger in head, bill, wing, tarsus, or tail length and body mass than females (Carboneras, 1992; González-Solis et al., 2000; Ristow & Wink, 1980). Interestingly, some storm petrels, appear to exhibit reversed sexual size dimorphism in body size (Castro et al., 2013; Croxall, 1995; Paiva et al., 2018; Warham, 1990). For instance, the European Storm Petrel *Hydrobates pelagicus* is an example of this reversed sexual size dimorphism, where females are larger than males in terms of wing and tarsus length (Castro et al., 2013; Warham, 1990). Although the differences in sexual size dimorphism in storm petrels are generally small, they still have the potential to impact the species' ecology. Sexual dimorphism in wing length or wing loading can influence lift and flight speed in open sea winds, leading to distinct movement patterns for males and females as they travel and forage during the breeding season. According to Paiva et al. (2018), the slightly longer wings of female Monteiro's Storm Petrels *Hydrobates monteiroi*, which were only about 3% longer than those of males, enabled them to forage more efficiently over extended distances. This led to segregation between the sexes, especially during the incubation period.

Recent studies, found that male and female Leach's Storm Petrel *Hydrobates leucorhous* not only exhibited different spatial foraging strategies during the incubation period (Mauck et al., 2022) but also have a sex-specific differences in parental care in relation to food provisioning to chicks, which is surprising for monomorphic species (Mauck et al. 2011; Tyson et al., 2022). On individual foraging trips, female Leach's Storm Petrel traveled further and spent a greater percentage of their foraging trips prospecting widely, regardless of the length of the trip (Mauck et al., 2022). Likewise, in years when krill is scarcer, female Wilson's Storm Petrels *Oceanites oceanicus* make longer foraging trips than males, enabling them to maintain chick-feeding rates comparable to males (Gladbach et al., 2009). One hypothesis for this difference may be that females are increasing their search for more or higher quality food in order to offset the cost of egg formation as eggs are exceptionally large relative to adult bodyweight, up to 22% (Montevecchi et al., 1983).

Mauck et al. (2011) observed male-biased effort in Leach’s Storm Petrel, with males spending more time incubating the egg than females, and when an egg failed to hatch, males kept incubating beyond the time in which females abandoned it. These findings are consistent with the hypothesis that, in order to prevent reproductive failure, males must compensate for the nutritional deficit that females initially experience during the chick-rearing period.

Regarding the chick rearing period, Tyson et al. (2022) discovered that males of Leach’s storm petrel provided food more frequently and contributed more to the overall feeding of the chicks than females. Females showed greater variation in trip duration within individuals, suggesting that they alternated more frequently between short, physically demanding trips that prioritized chick care and longer recovery trips that prioritized their own survival. Additionally, females were more likely to start longer journeys if they had just finished a shorter journey and had seen a chick in good health. However, males seemed to be better able to make numerous short trips, which led to more frequent and large overall contribution to chick feeding. These results are in line with the theory that energetic restrictions on females lead to male-biased provisioning in monomorphic species, and they are probably responsible for similar patterns in other long-lived species with high adult survival rates.

Table 2.3 Summarized breeding information for all storm petrel species

Species	Family	Nest type	Incubation period (days)	Fledging period (days)	References
Wilson's Storm Petrel *Oceanites oceanicus*	Oceanitidae	Burrow, crevice or natural hole	33-53	51-97	Roberts (1940), Beck and Brown (1972), Croxall (1981), Marchant & Higgins (1990), Warham (1990), Warham (1996)
White-vented Storm Petrel *Oceanites gracilis*	Oceanitidae	Crevices or below rocks, some of them covered by dense bushes; Cavities formed inside saltpetre formations, as in Markham's storm Petrels; Crevices in gypsum formations	No data	No data	Marin (1982), Schlatter and Marin (1983), Carboneras (1992), Hertel and Torres-Mura (2003), Barros et al. (2020)
Pincoya Storm Petrel *Oceanites pincoyae*	Oceanitidae	Unknown	No data	No data	This species is exclusively documented through at-sea observations in the region of Chile, with the additional discovery of two specimens collected inland at El Bolson, Argentina (Harrison et al., 2013). The prevailing theory proposes that this species is a resident of the mentioned area, and there are speculations about its potential breeding locations, which include islands, sea cliffs, or even inland sites (Harrison et al., 2013).
Grey-backed Storm Petrel *Garrodia nereis*	Oceanitidae	Burrow in vegetation, crevices in rocks	40-45	75	Marchant & Higgins (1990), Warham (1990), Warham (1996)
White-faced Storm Petrel *Pelagodroma marina*	Oceanitidae	Burrow	53.7 (46-60)[1], 51.7(38-53)[2]	52-67,80	Marchant & Higgins (1990), Warham 1990, Warham (1996) [1] Campos & Granadeiro (1999) [2]Underwood & Bunce (2004)
White-bellied Storm Petrel *Fregetta grallaria*	Oceanitidae	Burrow, crevice or natural hole	40	68	Marchant & Higgins (1990), Warham (1990), Warham (1996)
Black-bellied Storm Petrel *Fregetta tropica*	Oceanitidae	Crevice or natural hole (in thick vegetation or in peat)	35-44	55, 65-71	Beck & Brown (1971), Marchant & Higgins (1990), Warham (1990), Warham (1996)
New Zealand Storm Petrel *Fregetta maoriana*	Oceanitidae	Burrows under vegetation	No data	No data	It was previously believed that the species had gone extinct, as it had not been sighted since 1850. However, in a remarkable conservation achievement, the species was rediscovered in 2003 flying around its sole breeding site, the offshore island Te Hauturu-o-Toi. This rediscovery occurred after successful cat and rat eradication efforts on the island in the early 2000s (Stephenson et al., 2008; Rayner et al., 2015).
Polynesian Storm Petrel *NesoFregetta fuliginosa*	Oceanitidae	Crevice or natural hole under vegetation	No data	No data	Carboneras (1992)
European Storm Petrel *Hydrobates pelagicus*	Hydrobatidae	Crevice or natural hole	41	66	Warham (1990), Warham (1996), Cramp & Simons (1977)
Cape Verde Storm Petrel *Hydrobates jabejabe*	Hydrobatidae	Crevice mainly in mountainous sites and steep cliffs	No data	No data	Hazevoet (1995), Semedo et al. (2021)

Band-rumped Storm Petrel *Hydrobates castro*	Hydrobatidae	Burrow, crevice or natural hole	42	64-78	Allan (1962), Harris (1969), Warham 1990, Carboneras (1992)
Monteiro's Storm Petrel *Hydrobates monteiroi*	Hydrobatidae	Crevice or natural hole	No data	No data	Bolton et al. (2008), Meirinho et al. (2014)
Matsudaira's Storm Petrel *Hydrobates matsudairae*	Hydrobatidae	Burrow	No data	No data	Marchant & Higgins (1990), Carboneras (1992), del Hoyo et al. (1992)
Black Storm Petrel *Hydrobates melania*	Hydrobatidae	Burrow, crevice or natural hole	No data	No data	Carboneras (1992), Warham (1990)
Ashy Storm Petrel *Hydrobates homochroa*	Hydrobatidae	Crevice or natural hole	44.8 (42-59)	84.4 (72-119)	Ainley (1974), Ainley (1984), Ainley (1995), Warham (1990), Warham (1996),
Least Storm Petrel *Hydrobates microsoma*	Hydrobatidae	Crevice or natural hole			Ainley (1984), Carboneras (1992)
Wedge-rumped Storm Petrel *Hydrobates tethys*	Hydrobatidae	Crevice or natural hole under vegetation	No data	76	Carboneras (1992), del Hoyo et al. (1992)
Townsend's Storm Petrel *Hydrobates socorroensis*	Hydrobatidae	Burrow, crevice	No data	No data	Howell (2012)
Ainley's Storm Petrel *Hydrobates cheimomnestes*	Hydrobatidae	Burrow, crevice			Howell (2012)
Leach's Storm Petrel *Hydrobates leucorhous*	Hydrobatidae	Burrow, crevice or natural hole	43.3(37-50)	56-79	Ainley et al. (1974), Vermeer et al. (1988), Ainley et al. (1990), Marchant & Higgins (1990), Warham (1990), Huntington et al. (1996), Warham (1996)
Swinhoe's Storm Petrel *Hydrobates monorhis*	Hydrobatidae	Burrow	No data	No data	Carboneras (1992)
Guadalupe Storm Petrel *Hydrobates macrodactylus*	Hydrobatidae	Burrow at high elevation in soft soil under pines and cypress	No data	No data	The Guadalupe Storm Petrel, once abundant, has not been seen since 1912 despite various search efforts. It may have been driven to extinction by feral cats and habitat destruction caused by goats. However, it cannot be confirmed as Extinct due to the absence of comprehensive surveys since 1906 (BirdLife International, 2023b)
Tristram's Storm Petrel *Hydrobates tristrami*	Hydrobatidae	Burrow, crevice or natural hole	39-55	74-100	Warham (1990), Carboneras (1992), Marks & Leasure (1992), McClelland et al. (2008)
Markham's Storm Petrel *Hydrobates markhami*	Hydrobatidae	Fissures and cavities found under the surface on the salt flats	No data	No data	Warham (1990), Carboneras (1992), Torres-Mura & Lemus (2013), Schmit et al. (2015), Barros et al. (2019)
Fork-tailed Storm Petrel *Hydrobates furcatus*	Hydrobatidae	Burrow, crevice or natural hole	40	58	Boersma et al. (1980), Warham (1990), Warham (1996), Drummond & Leonard (2009),
Ringed Storm Petrel *Hydrobates hornbyi*	Hydrobatidae	Cavities in gypsum outcrops or salt cavities	No data	No data	Carboneras (1992), Barros et al. (2018), Medrano et al. (2019)

2.3. CONCLUSION

My review documented and summarized, for the first time, a thorough list of studies identifying the foraging and breeding behaviour of storm petrels, an area in which the knowledge is scarce. Many basic ecological questions remain unanswered for most species of storm petrels, requiring future research.

The two families (Oceanitidae and Hydrobatidae) have general physical distinctions, although it there is still a need to research with rigorous methods whether and how these variations translate to differences in foraging behaviour (del Hoyo et al., 1992). When compared to other species of the order Procellariiformes, besides the obvious difference in size, their morphology also differs greatly, resulting in distinctive fluttery flight and a unique foraging behaviour as described in this review.

Although storm petrels have been observed and studied at sea for years, information on their behaviour and ecology has gathered slowly. Overall, a small number of studies on individual foraging strategies of storm petrels have been published, and the majority of these studies are ship-based observations. Nonetheless, in the last ten years, there has been an increasing number of published papers on the foraging behaviour of these smaller species, reflecting the technology advancement and miniaturization of tracking devices. The first study was published in 2014, with 14 more published since then up to and including 2022. However, all these studies focus on Hydrobatidae species, with the exception of only one published study, with the White-faced Storm Petrel, on its foraging movements and diet in the Northeast Atlantic (Alho et al., 2022). We also concluded that in the total number of studies on this subject, using tracking devices, 80% of them are focused on the species *Hydrobates leucorhous* (N = 7) and *H. pelagicus* (N = 5). One reason for this may be due to the fact that the former is the most widespread storm petrel and the latter has >95% of its breeding range concentrated in Europe, with easily accessible and well-studied colonies. Furthermore, the same tendency has also be seen in published studies of storm petrel diet, which have increased in recent years. The ship-based studies allow for the observation of the context in which seabirds forage, such as interactions with conspecifics or prey and can be highly complemented by high-resolution tagging methods that provide fine-scale behavioural information (e.g., diving, area restricted searching) not only during the breeding season but also year-round data (Halpin et al., 2018). Associating the locations of specific behavioural occurrences with environmental characteristics is a potential approach that could help us better understand the mechanics driving the storm petrel behaviour.

How storm petrels use their sense of smell to forage at sea and interact in colonies is one of the most researched aspects of their behaviour. It is thought that the sense of smell in these birds is more developed and also varies within the species range. Various olfactory skills or adaptations may contribute to the foraging methods used by distinct species in varied contexts. This is consistent with various at-sea observations that smaller, cryptic species like prions and storm petrels responded strongly to DMS-scented slicks than larger species, like albatrosses (Nevitt, 2000). For instance, if storm petrels, have superior olfactory abilities, they may be able to discover and exploit prey patches before larger species arrive. Furthermore, because they are inconspicuous, they may be more difficult to detect by potential competitors.

Different seabird groups have quite different levels of development in their species-specific communication habits, particularly colonial nesting seabirds, that choose nesting habitat based on public information. Vocalizations are used in territorial and sexual contexts in crevice- and burrow-nesting Procellariiformes, as is the case with storm petrels.

Comprehending how these social cues affect the behaviour of each storm petrel species, can be crucial in the development of protocols for restoration colonies of this group. When colonies go extinct, social cues that indicate the quality of nesting locations are lost. Storm petrels are well known for being attracted to recordings of their calls, and efforts to establish new colonies through this type of social attraction have been successful (Bolton et al., 2004; Podolsky & Kress, 1989).

Importantly, future research efforts should be focused on understand the basic ecology of most species of storm petrels. As the knowledge gaps identified here are addressed, our understanding about foraging and breeding behaviour in storm petrels will increase.

CHAPTER 3

REVEALING THE FORAGING MOVEMENTS AND DIET OF THE WHITE-FACED STORM PETREL *PELAGODROMA MARINA* IN THE NE ATLANTIC

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3.1. ABSTRACT

The White-faced Storm Petrel *Pelagodroma marina* has a widespread distribution, although virtually nothing is known about their feeding ecology and distributions at-sea. To describe their foraging areas, a total of 77 birds were equipped with 1 g-GPS loggers on Selvagem Grande, Madeira, Portugal (30° 09′ N, 15° 52′ W), during the 2018 and 2019 breeding seasons. We also assessed the diet of White-faced Storm Petrel by analysing 17 faecal samples from chicks and 1 regurgitation from an adult using DNA metabarcoding techniques. Additionally, we collected body feathers from ten White-faced Storm Petrel chicks to determine mercury concentration. White-faced Storm Petrel fed mainly in deep oceanic waters, travelling up to 400 km from the colony, and did not concentrate in any well-defined, population-level foraging hotspots. Some individuals foraged along the edge of the shelf, near the African coast and the Canary Islands, especially during chick rearing. The duration of foraging trips and the total distance travelled,were, on average, 5.1 days and 723 km during the incubation period and 3.0 days and 578 km during chick rearing. The diet of White-faced Storm Petrel was dominated by fish and cephalopods (crustacean prey were not detected), with Myctophidae (FO = 71%) representing the main fish family. White-faced Storm Petrel often consume mesopelagic fish, in line with their preference for deep oceanic waters and with a small difference in at sea behaviour (i.e., travel speed) between the diurnal and nocturnal period. The relatively high concentrations of mercury accumulated in body feathers of White-faced Storm Petrel chicks (3.45 ± 1.44 mg kg^{-1} dry weight; range1.68–6.01 mg kg^{-1}) support the idea that White-faced Storm Petrel raise their chicks mostly on mesopelagic prey from deep pelagic areas.

3.2. INTRODUCTION

Seabirds represent an important component of marine trophic networks worldwide (Fauchald, 2009). They are major consumers in marine ecosystems (Brooke, 2004a,2004b; Furness, 1978) and use foraging areas ranging from tens to thousands of kilometres from their breeding grounds (Brooke, 2004a; Coulson, 2002). During the breeding season, seabirds are central place foragers, having to commute regularly between foraging locations and the colony, to attend their eggs or feed their chicks. The at-sea distributions of most seabirds are linked to spatial distribution of prey, their abundance, and availability (Depot et al., 2000; Hunt & Schneider, 1987; Fauchald et al., 2000). The diet of seabirds can reflect changes that occur at lower trophic levels, and thus, seabirds can be used as indicators helping to monitor the marine environment (Romero et al., 2021). Information on at-sea behaviour and space-use of pelagic seabirds is essential to understand their role in ocean ecosystems and is also increasingly used to inform marine spatial planning (Camphuysen et al., 2012; Oppel et al., 2018).

In recent years, bird-borne GPS devices have provided new insights into the spatial distribution and movement patterns for many large- and medium-sized seabird species at sea (BirdLife, 2020; Yoda, 2019). Although there has been much progress in the miniaturization of tracking devices, foraging areas for the small procellariiform seabirds are still largely unknown (Oro, 2014; Rodríguez et al., 2019). However, in the last few years, lightweight (~ 1 g) GPS devices have become available, which now allow tracking even the smallest seabird species over extended periods of time (Bolton, 2021; Hedd et al., 2018; Rotger et al., 2020).

The White-faced Storm Petrel *Pelagodroma marina* is a small burrow-nesting seabird (40–70 g; Marchant & Higgins, 1990) of the Hydrobatidae family, comprising six subspecies, found in Atlantic, Pacific, and Indian Oceans in both Hemispheres (del Hoyo et al., 1992). Except for few breeding pairs in the Canary Islands (ca. 50 pairs, Rodríguez et al., 2003), the global population of the endemic European subspecies (*Pelagodroma marina hypoleuca*) is confined to a small archipelago, the Selvagens Islands, in the North-east Atlantic (Campos & Granadeiro, 1999; Silva et al., 2015). Although further studies are required to confirm the actual population in the Selvagens archipelago, in 1996, population was estimated at 61,000 breeding pairs, of which 36,000 were counted in Selvagem Grande for the same year (Campos & Granadeiro, 1999).

Most studies on White-faced Storm Petrels have focused on breeding biology (Richdale, 1943–1944; Campos & Granadeiro, 1999; Menkhorst et al., 1984; Underwood & Bunce, 2004). Their at-sea distribution is largely unknown, but ship-based observations report that White-faced Storm Petrels are generally seen foraging over continental shelves (Cramp & Simmons, 1997; Rankin & Duffey, 1948; Spear et al., 2007; Warham, 1990). In contrast, an analysis of stable isotopes of carbon in toe-nails of the Selvagem Grande population suggests that birds probably forage over the deep ocean around the Selvagens, rather than feeding close to the African coast (Furtado, et al. 2016).

White-faced Storm Petrels are solitary-feeders and surface foragers, pattering the water with their long legs with out-stretched wings (Spear, et al. 2007; Watson et al., 1986; Warham, 1990). The diet of White-faced Storm Petrels consists mostly of small fish, pelagic crustaceans, and surface plankton (e.g., Brooke, 2004a,2004b; Imber, 1984; Marchant & Higgins, 1990; Spear et al., 2007). The species appears to be opportunistic (Spear et al., 2007), feeding both nocturnally and diurnally on a diverse array of Myctophidae fishes, but also pelagic fishes (e.g., Bregmacerotidae), crustaceans (e.g., Hyperiidea, Euphausiid, crab megalops), and other non-cephalopods invertebrates (e.g., water-striders *Halobates* spp., *Janthina* sp.). However, information about the feeding ecology of White-faced Storm Petrels from the North Atlantic is very scarce (Waap, 2015).

DNA metabarcoding of faecal samples is a non-invasive and robust method for identifying prey taxa (Buglione et al., 2018; De Barba et al., 2014; Symondson, 2002). With the development of high-throughput sequencing techniques (HTS) of DNA barcodes, it is now possible to detect DNA sequences from degraded biological material (Taberlet et al., 2012; Valentini et al., 2009), including from faeces. The emergence of such techniques opens promising opportunities to gather information on the diet of these small seabird species, avoiding the use of intrusive methods (Symondson, 2002).

Seabirds that rely extensively on mesopelagic prey tend to display high mercury concentrations compared to species with an epipelagic diet (e.g., Carravieri et al., 2018; Furtado et al., 2019, 2021; Kim et al., 1996; Monteiro & Furness, 1995;). This is due to the higher rate of microbial-mediated methylation of mercury in sub-thermocline low oxygen waters (Choy et al., 2009). Furthermore, pelagic seabirds show higher mercury concentrations as compared to coastal species (Monteiro & Furness, 1995; Monteiro et al., 1996b). Determination of feather mercury concentration hence allows further insights into the diet of seabirds, as mercury is deposited during feather growth, reflecting accumulation through diet over this period (Monteiro & Furness, 2001).

Here, for the first time, we examine the foraging movements of White-faced Storm Petrels in the NE Atlantic using GPS devices, during the incubation and chick rearing periods of 2 consecutive years. We also briefly describe the prey delivered during chick rearing by examining chick faecal samples using DNA metabarcoding. In addition, we report the mercury levels in chick body feathers in Selvagem Grande, reflecting the concentration of this heavy metal in prey obtained in the foraging areas used during chick rearing (Furtado et al., 2021; Stewart et al., 1997).

3.3. METHODS

3.3.1 STUDY AREA

Fieldwork was carried out on the island of Selvagem Grande (30° 09′ N, 15° 52′ W) (Fig. 3.1), the largest (245 ha) of the three islands which constitute the Selvagens Nature Reserve. Selvagem Grande is located in the North-east Atlantic, ca. 300 km south of the Island of Madeira (Portugal) and consists of a flat plateau surrounded by cliffs. The White-faced Storm Petrel breeds in burrows located in two well-defined areas of sandy soil in the plateau.

3.3.2 GPS TRACKING

In 2018 (April to May) and 2019 (April to June), a total of 65 White-faced Storm Petrels were captured at their nests during incubation, and equipped with 0.95 g GPS devices (Pathtrack Ltd., UK). Between May and June 2019, another 12 individuals were captured after feeding their chicks, using drop-traps set at the entrance of their burrows. Individuals were only tracked once, during the course of the study and 41% recorded more than one trip.

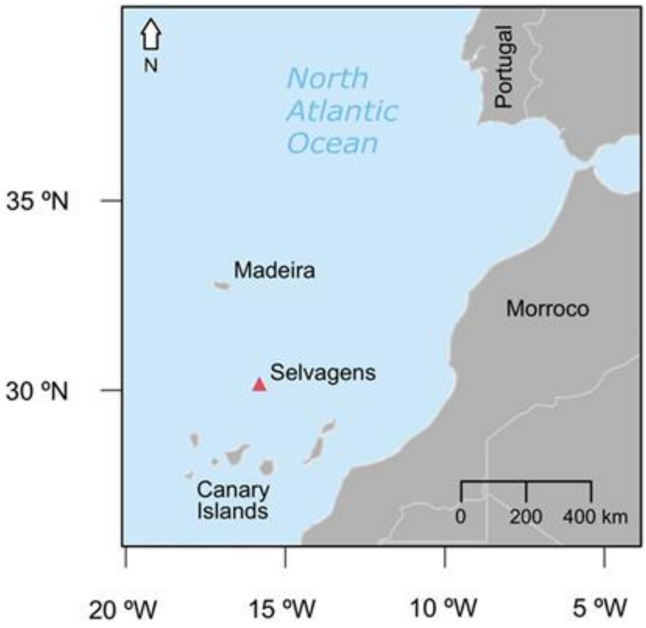


Fig. 3.1 Study area in the NE Atlantic, showing the location of Selvagem Grande (red triangle)

The GPS devices were attached to the base of the four central tail feathers using three narrow strips of TESA tape. The devices and attaching material weighed 1.1 g, corresponding to 1.9–2.4% of the body mass of tagged birds, below the 3% threshold above which it is believed the behaviour of birds may be affected (Phillips et al., 2003). Total handling time was kept to a minimum (less than 10 min) and birds were returned to their burrows immediately afterwards to resume incubation or until leaving the chick.

During the first deployments in 2018 (incubation period, *n* = 23 deployments), GPS devices were set to record a location every 3 h, but subsequently we increased the frequency of locations to two fixes per hour (*n* = 15). In 2019, still during the incubation period, GPS devices (*n* = 27) were programmed to take fixes every hour. Shorter trips were expected during chick rearing, and therefore, we programmed 8 GPS devices to record a location every hour and four GPS devices were set to record a location every half hour. Prior to GPS deployment, a set of birds in nests were marked with a small white patch in the head. Nests were then inspected daily to avoid fitting GPS devices on individuals who had recently returned from foraging trips. In addition, a group of control nests (*n* = 30) was chosen and also monitored regularly to evaluate any impact of GPS on behaviour by comparing duration of absences from the nest (i.e., trip duration) with those of deployed birds. We only checked controls during the incubation period. We tested for differences in trip duration between tagged birds and control group, using a generalized linear model (GLM) with a Poisson distribution.

3.3.3 GPS DATA PROCESSING

All GPS data were informally scanned for the presence of unrealistic fixes, identified as very large displacements associated with sudden changes in direction. These points (< 10) were eliminated before any analysis. All tracks from a single individual were split into individual trips, setting the start of the trip as the first fix obtained at more than 10 km from the colony, and the end if a fix was within 20 km from the colony (without any subsequent point further away from the colony). Several trips (25 out of 55) were not complete, due to battery failure (often in the end of the trip) or to other unknown cause (in this case, creating some gaps in the trips). Based on the degree of completeness of the trips, and on our daily attendance records at each nest, some of the trips were used to calculate trip metrics (last GPS fixes missing only when returning birds were very close to the colony, $n = 55$ trips). Incomplete trips were also used to calculate kernel utilization distributions when areas of intensive use could be clearly identifiable ($n = 48$) or to calculate other trip metrics (e.g., maximum trip distances) when tracking data clearly indicated that birds were clearly on their return to the colony ($n = 46$). We considered complete trips ($n = 17$ for incubation; $n = 13$ for chick rearing) to calculate total distance travelled (km), maximum distance (km) from the colony and trip duration (h). In addition, we also used nearly complete trips based on the quality of the trips for each trip characteristic parameter [total distance travelled ($n = 10$ for incubation; $n = 5$ for chick rearing), maximum distance ($n = 11$ for incubation; $n = 5$ for chick rearing), and trip duration ($n = 6$ for incubation; $n = 4$ for chick rearing)]. Finally, for the identification of foraging areas and to calculate the depth at foraging areas, we used data from complete tracks ($n = 17$ for incubation; $n = 13$ for chick rearing) and nearly complete trips ($n = 14$ for incubation; $n = 4$ for chick rearing).

Kernel utilization distributions were calculated for the incubation and chick rearing period on projected coordinates (UTM zone 28N, datum of Selvagens, EPSG = 2943) linearly interpolated at 1 h, using adehabitatHR package (Calenge, 2006), setting the smoothing parameter (h) at 10,000 m (close to the average step length recorded per hour, see “Results”). We excluded from this analysis all interpolated points, whenever their time difference was ≥ 4 h. All fixes were then interpolated at 1 h intervals for subsequent analysis. To assess the differences in speed (hence total extent) estimated at different sampling intervals, we resampled all trips obtained at 0.5–1 h and 2 h intervals, and calculated the mean speeds in each case. As expected, shorter sampling intervals delivered higher estimates of speed (0.5 h = 9.4 ± 5.5 km h^{-1}) than those estimated at longer periods (1 h = 8.9 ± 5.3 km h^{-1}; 2 h = 8.4 ± 5.4 km h^{-1}), but the differences were small, particularly between 1 and 2 h (ca. 5.8%). Since all trips were interpolated at 1 h (hence eliminating biases due to 0.5 h sampling intervals), we did not undertake any correction to deal with differences in fix intervals. All fixes were classified as diurnal or nocturnal according to the civil twilight, i.e., setting them as nocturnal whenever the fix was obtained when the sun was – 6° or less below the local horizon and diurnal otherwise [function crepuscle in maptools R package (Bivand & Lewin-Koh, 2020)]. To quantify any difference in sea-floor depth between incubation and chick rearing, we intersected the 50% kernel utilization distribution (UD) of each individual with the bathymetric data obtained from ETOPO1 Global Relief Model (at 1 arc-min resolution, https://www.ngdc.noaa.gov/mgg/global), from which we calculated an average value of depth per individual. We also identified all fixes lying within the 50% UD of all individuals during incubation and chick rearing, to quantify the proportion of fixes in these areas during the day and during the night in each period.

3.3.4 CHICK DIET DETERMINATION WITH DNA METABARCODING

DNA isolation and sequencing

In 2019, we collected faecal samples from 28 chicks at their nests. The mean age of the chicks sampled was 19.6 ± 9.4 days (range 3–33). A tinfoil sheet was placed at the bottom of the nest chamber each morning (after the adult had left the nest), where chicks would defecate naturally. The nest chamber was inspected regularly during the morning period until the faecal samples were collected. If during that period, the chick had not defecated, the tinfoil was retrieved and sampling would be resumed the following day. Faecal samples were collected with a plastic spatula and stored in 2 mL tubes with absolute ethanol and stored at – 20 °C. One spontaneous regurgitate from an adult about to feed its chick was also included in diet analysis. DNA was isolated from each sample with a Norgen Stool DNA isolation kit (cat#27600, Norgen Biotek, Canada). The tubes were centrifuged for 1 min at 13,000 rpm and ethanol was carefully removed by aspiration with a micropipette before transferring the solid phase into the bead tubes. Samples were incubated in lysis buffer with gentle vortex for 1–2 h at room temperature before horizontal bead beating in a vortex at full speed. DNA was eluted in 65 µL of elution buffer at the final step of the protocol. The elution buffer was preheated at 70 °C and allowed to incubate at room temperature for 30 min before centrifuging. DNA samples were evaporated with SpeedVac to a final volume of 20 µL, using then Qubit 2.0 [Invitrogen with Qubit dsDNA HS Assay kit (Thermo Fisher Scientific)] to measure final DNA concentration. Samples with less than 1 ng/µL were discarded (8 samples) and the remaining (20 samples) were used for DNA metabarcoding. Libraries were prepared by AllGenetics and Biology SL (http://www.allgenetics.eu), aiming to target the main prey groups with the 16S gene: fishes/cephalopods and crustaceans. Primers and the blocking primer used as well as conditions for DNA amplification by polymerase chain reaction (PCR) are provided in the supplementary material 1 (Annex B). All samples that produced a PCR product were sequenced in NovaSeq PE250 (Illumina). Amplifications with the crustacean primers were successful for the regurgitate sample but failed for the faecal samples, despite several rounds of optimization. The DNA concentrations obtained from the regurgitate sample were high (24.2 ng/µL), but it was very low for several faecal samples (mean 7.5 ng/µL, range 1.03–30.4 ng/µL), which likely added difficulties to obtain successful amplification of DNA fragments. DNA obtained from faeces is expected to present higher degradation as compared to stomach content due to longer digestion time of prey tissues (Sousa et al., 2019).

Sequence analysis and taxonomic assignment

Sequence data were processed under Qiime2-2021.4 pipeline (Bolyen et al., 2019) with the DADA2 plugin (Callahan et al., 2016) to trim primer sequences, filter reads by quality (Phred ≥ 20), merge paired-end reads (setting a minimum overlap of 50 bp for pairing forward and reverse reads), and collapse them into a list of unique Amplicon Sequence Variants (ASVs). ASVs were then classified with Qiime2 classify-consensus-vsearch (Bokulich et al., 2018; Rognes et al., 2016) with the 16S Midori UNIQ-NUC_GB244 database as reference (Machida et al., 2017), setting 0.8 as minimum identity and 0.7 as minimum cover (full list of commands are provided in Online Resource 1). Taxa assignments by vsearch were confirmed by querying ASVs against

GenBank with NCBI BLASTn (https://blast.ncbi.nlm.nih.gov/ Blast.cgi). Assignments to species level were confirmed if ASVs had a 98–100% match to the best hit in blastN or adjusted to the least common ancestor whenever other taxa were assigned with similar identity or no occurrence of the species in the North Atlantic was documented. Unassigned and non-target contaminant sequences were discarded from further analyses.

Mercury analysis

We collected eight-to-ten back body feathers from ten White-faced Storm Petrel chicks during the 2019 breeding season for quantification of total mercury. The mean age of the chicks sampled was 33.2 days (SD 2.44, range 30–36 days). These ten chicks were also included in the diet determination using DNA metabarcoding. The difference between faecal and feather sampling was 3.7 days (range 2–6 days). Feathers were clipped at the superior umbilicus of the feather, excluding the calamus, and stored in polyethylene bags. Samples were weighed on a Sartorius M5P micro balance (Sartorius AG, Goettingen) (mass between 0.441 and 3.020 mg, mean 1.23 ± 0.59 mg) and analysed according to the method described in Furtado et al. (2021). Total mercury in the body feathers was quantified by atomic absorption spectrophotometry with thermal decomposition (Costley et al., 2000) in LECO AMA-254 with a detection limit of 0.01 ng of mercury. At least two aliquotes of each sample were analysed, until the standard deviation was < 10%. Subsequently, the mean of the repeated mercury measurements was used for statistical analysis. Blanks were systematically run between samples (two procedural blanks). The mercury concentrations in procedural blanks were always below the detection limit of the equipment (0.01 ng of mercury). Precision and accuracy of the analytical method were evaluated by analysis of certified reference material (lobster hepatopancreas TORT-3; NRC, Canada). Reference values were of 0.292 ± 0.022 mg kg^{-1} dry weight (dw), and the mean determinations ± SD were 0.280 ± 0.176 mg kg^{-1} dw (n = 8). Thus, the recovery of the Certified Reference Material (CRM) was 95.9%. Results were corrected using the daily recovery efficiency of CRM.

Statistical analysis

Comparisons of trip metrics between individuals tracked during incubation and chick rearing were carried out using general linear models. We also compared the distance travelled by birds during the day and night in both reproductive phases, used linear mixed models (LMM), assuminga Gaussian error distribution. To do this, we calculated the distance travelled between consecutive points for each bird [i.e., travel speed (km h^{-1})] using time of day (daylight andnight, classified as above) and phase (incubation and chick rearing) as factors, and setting the individual as a random factor. We started with a full model (random effects and interaction between day and phase), and then compared it with increasingly simpler models, using ANOVA-like test for random and fixed effects. These tests were carried out using lmerTest (Kuznetsova et al., 2017) and lme4 packages(Bates et al., 2015) for R (R Core Team, 2021). We estimatedthe bearing of the position of each individual in relation to the colony at a distance of 10 km, and tested the uniformity in the direction of departure from the colony, using Rayleigh uniformity test in circular package (Agostinelli & Lund, 2017).

3.4. RESULTS

3.4.1 GPS RETRIEVAL

Overall, 66 out the 77 deployed GPS were recovered. All individuals tracked during the chick rearing period were recaptured at their nest. During incubation, nine birds could not be recaptured and eventually deserted their nest. Two birds lost the GPS attached. Four GPS did not deliver data due to device failure. From the 62 remaining GPS with data,we were only able to extract 55 trips for trip metrics calculation. There were no significant differences in trip duration between the recaptured birds with GPS and the control group [means (± SD): 6.5 ± 1.4 days (n = 109) vs 6.2 ± 1.7 days (n = 53), respectively, GLM $\chi^2_1 = 0.59$, $P = 0.44$].

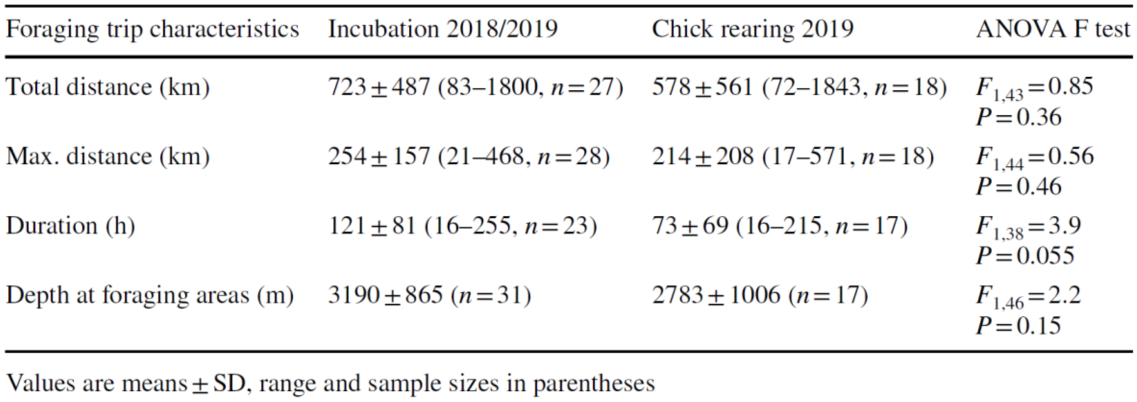
3.4.2 FORAGING TRIPS

Total distance travelled, maximum distance from the colony,and trip duration were not significantly different between years during the incubation period (ANOVA, $F_{1,25} = 0.78$,$P = 0.39$, $F_{1,26} = 1.16$, $P = 0.29$ and $F_{1,21} = 3.79$, $P = 0.06$), so data from the 2 years were pooled.

Trip characteristics during incubation and chick rearing are summarized in Table 3.1

and are based on 30 complete trips and 19 nearly complete trips recorded, for both breeding phases. No significant differences in total distance, maximum distance, and trip duration were found between breeding periods (all $P > 0.05$; Table 3.1). However, there was a tendency for more distant foraging trips during incubation [18 birds (67%) undertook foraging trips over 500 km and 10 individuals (37%) travelled over 1000 km] compared to the chick rearing period [seven birds (49%) undertook foraging trips over 500 km, and only three birds (17%) travelled over 1000 km] (see supplementary material 2, Fig. B1).

Table 3.1 Characteristics of foraging trips of White-faced Storm Petrel tracked with GPS devices from Selvagem Grande Island in 2018 and 2019 and comparisons between periods



Foraging trip characteristics	Incubation 2018/2019	Chick rearing 2019	ANOVA F test
Total distance (km)	723 ± 487 (83–1800, $n = 27$)	578 ± 561 (72–1843, $n = 18$)	$F_{1,43} = 0.85$ $P = 0.36$
Max. distance (km)	254 ± 157 (21–468, $n = 28$)	214 ± 208 (17–571, $n = 18$)	$F_{1,44} = 0.56$ $P = 0.46$
Duration (h)	121 ± 81 (16–255, $n = 23$)	73 ± 69 (16–215, $n = 17$)	$F_{1,38} = 3.9$ $P = 0.055$
Depth at foraging areas (m)	3190 ± 865 ($n = 31$)	2783 ± 1006 ($n = 17$)	$F_{1,46} = 2.2$ $P = 0.15$

Values are means ± SD, range and sample sizes in parentheses

Throughout the breeding period, birds were mostly associated with offshore pelagic areas (average depth > 2000 m; Table 3.1 and Fig. 3.2). Most trips targeted deep waters around the colony. During the chick rearing period, four birds foraged in the shelf edge/slope, two near the African coast and the others on the west side of Fuerteventura Island (Fig. 3.2b). Birds set off in all directions from the colony during the incubation period (Rayleigh uniformity test: test statistic = 0.29, $P = 0.06$, Fig. 3.2a), but tended to leave the island to the east during chick rearing (83° from the geographical north, Rayleigh uniformity test: test statistic = 0.53, $P = 0.002$). White-faced Storm Petrel did not seem to concentrate in any well-defined foraging hotspots (Fig. 3.2).

Birds travelled slightly but significantly faster during the night (effect of period: day = 6.6 ± 2.2 km/h, night = 8.4 ± 2.3 km/h, LMM, $t = 3.0$, $P = 0.004$, Fig. 3.3) and also faster during chick rearing (effect of breeding phase: incubation = 7.1 ± 2.3 km/h, chick rearing = 8.6 ± 2.0 km/h, LMM $t = 2.7$, $P = 0.01$), with no significant interaction ($t = 1.8$, $P = 0.08$). The 50% UD of all individuals tendedto contain slightly more diurnal than nocturnal fixes(day:night ratios, incubation = 1.20 (n = 1512 fixes); chick rearing = 1.49 (n = 558).

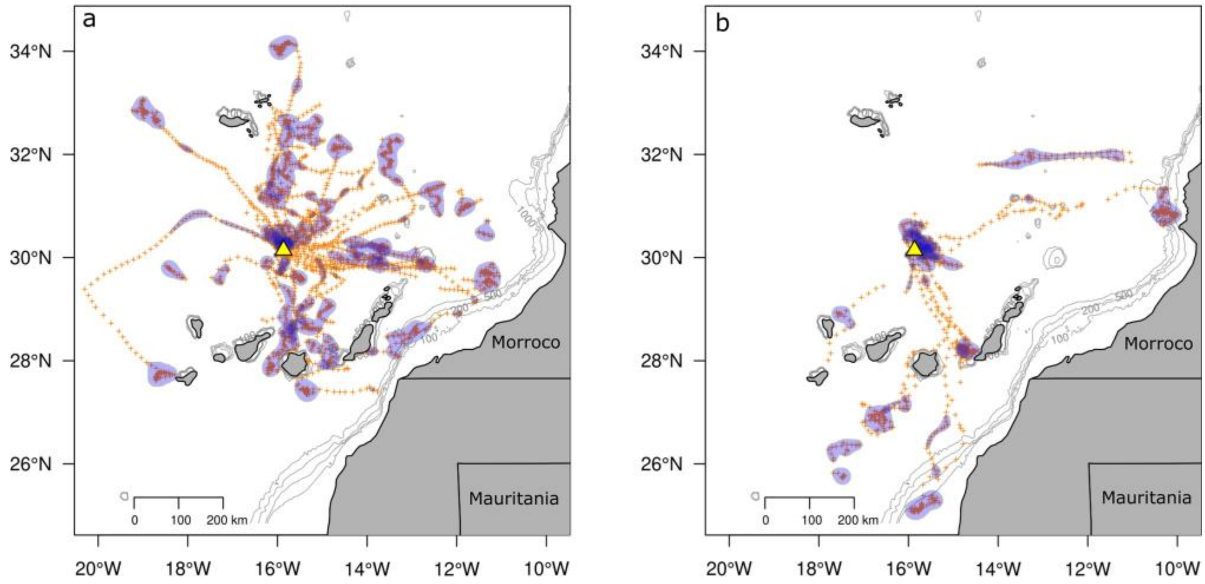


Fig. 3.2 Foraging trips of White-faced Storm Petrel during incubation (a) 2018 and 2019 (n = 31) and chick rearing (b) 2019 (n = 17) from Selvagem Grande and 50% utilization distribution of each individual. Selvagem Grande is represented with a triangle

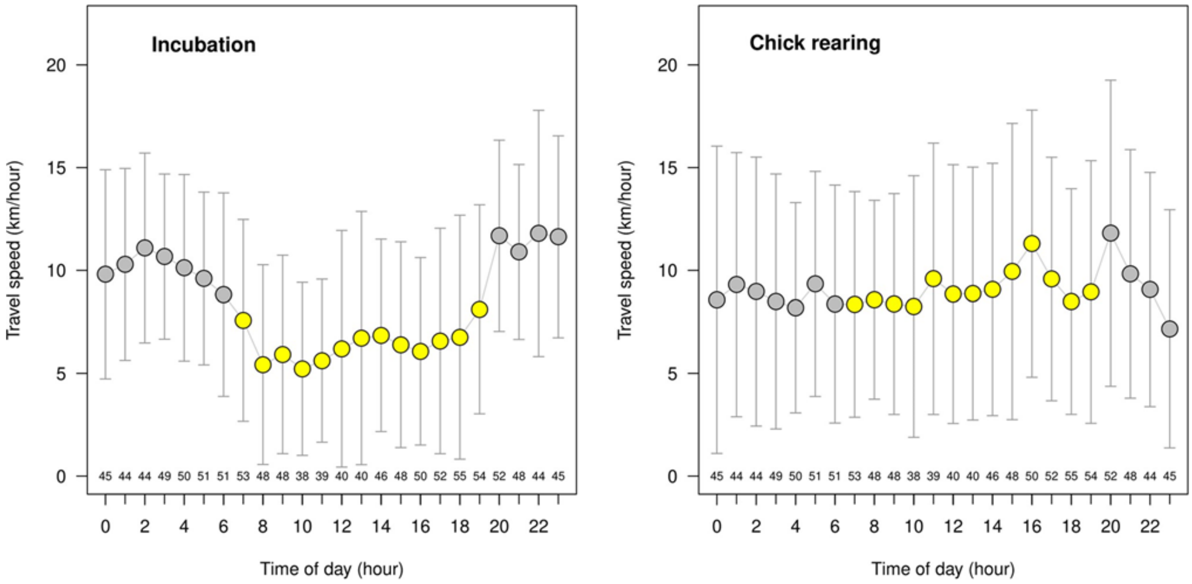


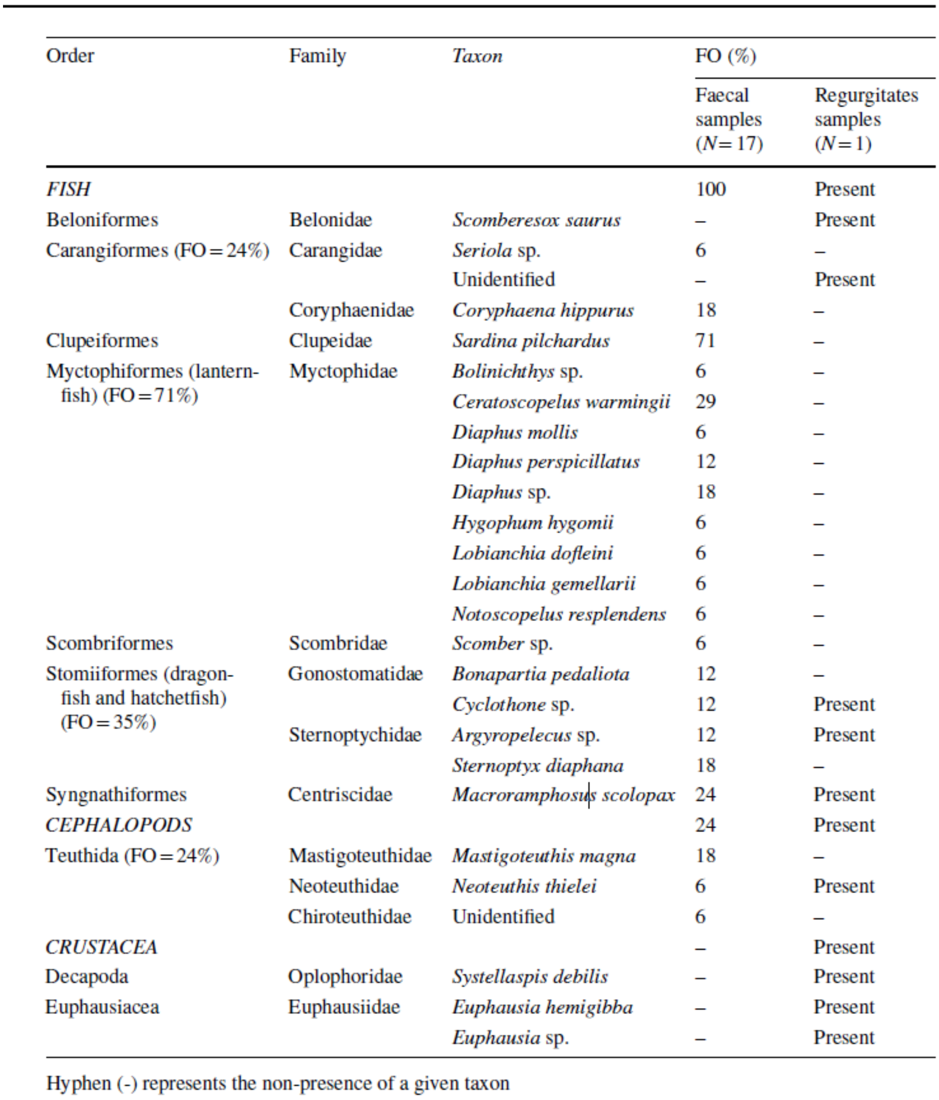
Fig. 3.3 Travel speed (speed, km h^{-1}) of White-faced Storm Petrel during incubation and chick rearing from Selvagem Grande during day and night. Samples sizes are indicated in the x-axis

3.4.3 DIET

Prey sequences were detected in 17 samples (out of 20) and they all contained fish. European pilchard *Sardina pilchardus* (Clupeidae) predominated in samples (FO = 71%), followed by Warming's lantern fish *Ceratoscopelus warmingii* (Myctophidae, FO = 29%) and Longspine snipefish *Macroramphosus scolopax* (FO = 24%) (Table 3.2). Myctophids were represented by 8 species, from 6 genus. Mesopelagic prey were present in 94% of the samples.

Cephalopods occurred in 24% of the faecal samples, with *Mastigoteuthis magna* being the most detected species. The regurgitate of the adult presented a high number of taxa (9 different prey), including some crustaceans.

Table 3.2 Frequency of (FO %) of prey in the diet of White-faced Storm Petrel during the chick rearing period as assessed from 17 faecal samples from chicks and 1 regurgitate from an adult



Order	Family	*Taxon*	FO (%)	
			Faecal samples (*N* = 17)	Regurgitates samples (*N* = 1)
FISH			100	Present
Beloniformes	Belonidae	*Scomberesox saurus*	–	Present
Carangiformes (FO = 24%)	Carangidae	*Seriola* sp.	6	–
		Unidentified	–	Present
	Coryphaenidae	*Coryphaena hippurus*	18	–
Clupeiformes	Clupeidae	*Sardina pilchardus*	71	–
Myctophiformes (lanternfish) (FO = 71%)	Myctophidae	*Bolinichthys* sp.	6	–
		Ceratoscopelus warmingii	29	–
		Diaphus mollis	6	–
		Diaphus perspicillatus	12	–
		Diaphus sp.	18	–
		Hygophum hygomii	6	–
		Lobianchia dofleini	6	–
		Lobianchia gemellarii	6	–
		Notoscopelus resplendens	6	–
Scombriformes	Scombridae	*Scomber* sp.	6	–
Stomiiformes (dragonfish and hatchetfish) (FO = 35%)	Gonostomatidae	*Bonapartia pedaliota*	12	–
		Cyclothone sp.	12	Present
	Sternoptychidae	*Argyropelecus* sp.	12	Present
		Sternoptyx diaphana	18	–
Syngnathiformes	Centriscidae	*Macroramphosus scolopax*	24	Present
CEPHALOPODS			24	Present
Teuthida (FO = 24%)	Mastigoteuthidae	*Mastigoteuthis magna*	18	–
	Neoteuthidae	*Neoteuthis thielei*	6	Present
	Chiroteuthidae	Unidentified	6	–
CRUSTACEA			–	Present
Decapoda	Oplophoridae	*Systellaspis debilis*	–	Present
Euphausiacea	Euphausiidae	*Euphausia hemigibba*	–	Present
		Euphausia sp.	–	Present

Hyphen (-) represents the non-presence of a given taxon

3.4.4 MERCURY

The mean mercury concentration in chick back body feathers was 3.45 ± 1.44 mg kg^{-1} dry weight ($n = 10$), with concentrations ranging from 1.68 to 6.01 mg kg^{-1} dw. Following the equation published by Ackerman et al. (2016), the average mercury concentration of chick feathers would correspond approximately to a blood mercury concentration of 0.43 ± 0.24 mg kg^{-1} wet weight (range 0.27–0.63 mg kg^{-1}).

3.5 DISCUSSION

In this study, we present novel data on foraging movements of the White-faced Storm Petrel during the incubation and chick rearing periods from the largest colony of this species in the North Atlantic. The White-faced Storm Petrel departed from the colony without a strong preference in directionality and used mostly deep oceanic waters. They seem to have a marked nocturnal activity during the chick rearing period, feeding mostly on mesopelagic prey, which is corroborated by the relatively high concentrations of mercury accumulated in feathers.

Individual foraging trips of White-faced Storm Petrel covered an average distance of more than 700 km while foraging during the incubation and more than 500 km during the chick rearing periods. Some individuals travelled more than 1000 km in one foraging trip during incubation, and further than 400 km off Selvagem Grande. Although remarkable that a small petrel such as the White-faced Storm Petrel is able to travel so far during the breeding season, this is consistent with recent tracking results for other small species of Procellariiformes. For instance, the Leach's Storm Petrel *Hydrobates leucorhous* and Fork-tailed Storm Petrel *Hydrobates furcatus*, both weighing ca. 50 g birds, are able to travel distances up to 1600 km from the colony during the breeding season (Bolton, 2021; Collins et al., 2022; Halpin et al., 2018; Hedd et al., 2018; Pollet et al., 2014). Rotger et al. (2020) also reported that Mediterranean Storm Petrels *Hydrobates pelagicus melitensis* in the Mediterranean Sea ranged up to 350 km from breeding colonies during incubation. As commonly observed in Procellariiformes (e.g., Cecere et al., 2013; Guilford et al., 2008), White-faced Storm Petrels made shorter foraging trips during chick rearing compared to incubation to ensure regular feed to their chicks (the lack of statistical significance is probably due to the small sample size and to the large variability in the tracking data).

Petrels are highly efficient flyers, using updrafts, slope, and dynamic soaring to exploit wind energy (Warham, 1990). Some small seabirds (e.g., Bulwer's petrel *Bulweria bulwerii*; Gadfly petrels *Pterodroma* spp.) often choose to fly with favorable side winds that enable them to travel at high ground speeds and low energetic cost (Dias et al., 2016; Ventura et al., 2020). Storm petrels, mostly the northern storm petrels (Family Hydrobatidae), use dynamic soaring to travel over the ocean surface (Pennycuick 1982; Warham, 1990) but this method does not seem to be used by White-faced Storm Petrel to any large extent (Cramp & Simmons, 1997; Erickson, 1955; Pennycuick, 1982). In fact, White-faced Storm Petrel most frequently exhibit a distinctive flight pattern when feeding as they hop using both feet along the surface of the water facing the wind with extended wings (Marchant & Higgins, 1990). This behaviour is used to a varying degree among species, and it seems to be related to the general morphological differences between species (del Hoyo et al., 1992; Sausner et al., 2016). Some species, such as the White-faced Storm Petrel, use pattering almost exclusively, whereas other species, such as Leach's Storm Petrel (*Hydrobates leucorhoa*), rarely use it (del Hoyo et al., 1992). Pattering is also prominent in the Oceanitidae family (southern storm petrels). Moreover, Sausner et al. (2016) suggested that species that pattering the most have low wing loading (mass (g)/total wing area (cm2)), low foot loading (relative foot size − mass (g)/foot area (cm2)), and a long tarsus in contrast to species that were classified as intermediate or least pattering (e.g., *Hydrobates leucorhous*). This might can explain differences in flight performance, as species increase flight speed with increasing wing loading. This unique flight behaviour and morphology (wide wings and very long legs and feet) may be limiting White-faced Storm Petrel capability of undertaking exceptionally long foraging trips as the *Hydrobates* species mentioned above do (e.g., Collins et al., 2022; Hedd et al., 2018; Pollet et al., 2014).

Many seabird species breeding in oceanic tropical environments are known to forage in multiple directions owing to the spatial unpredictability of prey (Hennicke & Mott et al., 2016; Oppel et al., 2015; Weimerskirch, 2014). A recent study by Oppel et al. (2018) showed that some families of seabirds, such as storm petrels, disperse widely at sea and exhibited large foraging ranges. Our data indicate that during the incubation period, White-faced Storm Petrels also seem to travel without directionality, not showing a clear choice for any well-defined foraging hotspots (the east directionality shown in chick rearing is probably due to the small sample size). This movement pattern suggests that while prey may be typically unpredictable in this area, they are widely distributed.

The oceanic areas of the subtropical eastern North Atlantic are characterised by warm sea surface temperatures and low productivity, differing from the nutrient-rich waters of the coastal upwelling of West Africa associated with the Canary Current (Cropper et al., 2014; Paiva et al., 2010). White-faced Storm Petrel does not seem to be associated with seamounts or core upwelling areas in the African coast, in contrast with other Procellariiform species from this and adjacent colonies. For example, Cory's shearwater *Calonectris borealis* from Selvagem Grande forage the oceanic domain around the islands, the African continental shelf (from Morocco to Mauritania), and the nearest seamounts (e.g., Alonso et al., 2012; Ramos et al., 2013; Romero et al., 2021). On the other hand, the Bulwer's petrel explores areas around the colony and waters close to the Azorean archipelago (mid-Atlantic) (Dias et al., 2016), but birds from the Canary Islands also use the shelf-break to forage during the breeding season (Rodríguez et al., 2013). Deserta and Madeira's petrel (*Pterodroma deserta* and *P. madeira*) perform very large clockwise foraging trips assisted by favourable winds, and use a large pelagic region around the archipelagos of Madeira and Azores (Ramos et al., 2016; Ventura et al., 2020). The distribution of White-faced Storm Petrels far from the continental shelf confirms the highly pelagic behaviour of this species. Notwithstanding, they also forage in the continental shelf edge and near the Canary Islands. Due to the influence of the Canary Current, the African shelf and shelf-break represent productive areas in the north-east Atlantic (Barton et al., 1998), which leads to enhanced productivity of the shelf edge areas (Hunt et al., 1999; Weimerskirch, 2007).

The diet of White-faced Storm Petrels, as assessed through DNA metabarcoding of chick faeces during the chick rearing period, was dominated by fishes and a few cephalopods species. The main fish family found was Myctophidae (FO = 71%), and is in accordance with the study by Spear et al. (2007) in the Pacific and by Waap (2015) in the North Atlantic. The presence of mesopelagic prey in the diet of surface seizing seabirds is striking. They are probably available to White-faced Storm Petrel during the night, when they ascend to more superficial waters to feed on zooplankton. Alternatively, they can be forced to the surface by underwater predators, such as whales, dolphins, and tuna, which are abundant in the region. Still, the presence of such prey is also frequent in the diet of other small seabirds that nest in the North Atlantic, such as Bulwer's Petrel, Madeiran Storm Petrel *Hydrobates castro*, and Leach's Storm Petrel (Carreiro et al., 2020; Hedd &

Montevecchi, 2006; Hedd et al., 2009; Monteiro et al., 1996; Waap, 2015; Waap et al., 2017; Zonfrillo, 1985). Cephalopods were the second most abundant group in the diet of White-faced Storm Petrel (FO = 24%), with *Mastigoteuthis magna* being the most detected species. The cephalopod species present occur mainly in mesopelagic or even bathypelagic environments, although some species are epipelagic when in larval or juvenile stages (Clarke, 1986).

The European pilchard, an epipelagic species, also occurred frequently (FO = 71%) in the diet of White-faced Storm Petrel. Sardines are abundant in coastal waters being one of the most abundant pelagic species off the NW African Coast (Machu et al., 2009). In the coastal (neritic) waters of the Madeira Archipelago, especially off the south coast of Madeira Island, there is a year-round fishery for small pelagic fishes, including the European pilchard. Fish larvae, e.g., of *Sardina pichardus*, from the spawning area of north- west Africa are known to be transported to the waters of the Canary Islands. This can explain the foraging movements of some tracked White-faced Storm Petrel near the African continental shelf edge and near the Canary Islands. Storm petrels in general are not usually observed foraging inshore, although the European Storm petrel (*Hydrobates pelagicus*) frequently does so (D'Elbee & Hemery, 1998; Poot, 2008).

Although crustaceans are known to be an important group in White-faced Storm Petrel diet (Croxall et al., 1997; Spear et al., 2007; Waap, 2015), we only recorded them in the adult regurgitate sample. None were recorded in the chick faecal samples. The efficiency of the crustacean DNA amplification in the faecal samples might have been reduced because of the lower yield of DNA extracted. Another hypothesis is that crustaceans were not detected, owing to a high degradation of their DNA which prevented PCR amplification. Due to longer gut retention, high assimilation, and digestion efficiency, samples derived from chick faeces contain more degraded DNA sequences, and hence, less identifiable DNA sequences than those obtained from adult regurgitates (e.g., Hilton et al., 2000; Wilson et al., 1989). The same PCR protocol applied to the regurgitate sample returned several crustacean species, which is consistent with the macroscopic observation of regurgitated tissues, containing about a dozen of small sized Euphausiidae (< 1 cm) partially digested.

The absence of crustaceans in the chick faeces may also result from parents selecting higher quality food for their offspring (Wanless et al., 2005). In Newfoundland and Nova Scotia, Leach's storm petrels rely heavily on mesopelagic fish while raising chicks (Hedd

& Montevecchi, 2006; Hedd et al., 2018), as these are energy-rich fish (Hedd & Montevecchi, 2006; Lea et al., 2002) but also smaller proportions of euphausiid and hyperiid crustaceans of lower energy content (Hedd & Montevecchi, 2006). Conversely, in winter, their diet likely consisted of a significant proportion of crustaceans (Hedd & Montevecchi, 2006). Wilson's Storm Petrel *Oceanites oceanicus* also adjust their diet for more energetic prey during the chick rearing period, increasing the amount of myctophid fish and decreasing of krill (Gladbach et al., 2007; Quillfeldt, 2002).

Seabirds that are more specialized in mesopelagic prey, such as several species of *Oceanodroma*, *Fregetta*, *Pterodroma*, and *Bulweria*, tend to forage more frequently in offshore/oceanic waters and are markedly nocturnal (Brooke & Prince, 1991; Spear et al., 2007; Warham, 1990). Mesopelagic fish (e.g., Myctophidae, Photichthyidae, and Sternoptychidae) and cephalopods display diel vertical migrations that make them available to shallow divers at night (Gjøsaeter & Kawaguchi, 1980; Watanabe et al., 1999). These groups were frequent in the diet of White-faced Storm Petrel, which fits well with the observed high activity during the night. Our results showed that White-faced Storm Petrels seem to behave differently during the incubation period than during the chick rearing period. Due to a higher travel speed during the night in the incubation period, we hypothesized that White-faced Storm Petrel may be pattering less, and therefore, it may not be feeding as much at night as during the chick rearing period. It is possible that during the chick rearing as this is a more energetically demanding time, birds tend to search for prey both day and night, presenting similar travel speed during day and night at this breeding period. This fits also with the finding that the birds consumed both mesopelagic and epipelagic prey during the chick rearing period. This is also in line with their oceanic distribution while foraging, since mesopelagic fish are scarce or absent in the continental shelf and other shallower areas (Gjøsaeter & Kawaguchi, 1980; Nybakken, 2001; Pusch et al., 2004).

The chicks of White-faced Storm Petrel showed no significant differences in mercury concentration in body feathers compared to the chicks of Bulwer's Petrel, a specialist predator of mesopelagic prey (Waap et al., 2017) from the Deserta Grande, Madeira (275 km north of our study site), that showed a mercury concentration in body feathers of 4.38 ± 1.69 mg kg^{-1} dw in 2018 (mean ± SE, Furtado et al., 2021) (Welch's *t* test, $t = -1.491$, $df = 0.28$, $P = 0.148$). Seabirds feeding on mesopelagic prey present higher mercury concentrations in feathers than those feeding predominantly on epipelagic prey (Bond &

Diamond, 2009; Carravieri et al., 2018; Furtado et al., 2019, 2021; Kim et al., 1996; Monteiro & Furness, 1995; Monteiro et al., 1996b;). Hence, mercury measurements in feathers support the idea that White-faced Storm Petrels raise their chicks mostly on mesopelagic prey. In addition, deep water pelagic fishes are known to accumulate higher mercury concentrations than nearshore species (Burger & Gochfeld, 2000; Monteiro et al., 1996b).

Currently, there are insufficient data to evaluate the cumulative effects of mercury for many seabird populations. A recent study by Pollet et al. (2017) found that levels of mercury in blood of adult Leach's storm petrels (0.78 ± 0.43 mg kg^{-1} wet weight) were relatively high (compared to other species of seabirds from the same region), and yet did not appear to adversely affect their offspring development or the return rates of adults from previous years. It is also expected that the mercury concentration in feathers found in our study (corresponding to 0.43 ± 0.24 mg kg^{-1} wet weight in blood, following Ackerman et al., 2016) will not cause negative effects in chicks.

Smaller seabird species, such as White-faced Storm Petrels, can reflect changes that occur at lower trophic levels and thus be potential bioindicators of marine conditions and therefore sentinels to environmental changes which respond at a faster speed compared to larger seabirds (Grémillet & Charmantier, 2010). This study presents the first baseline information on the foraging ecology of this species, and one of the still few studies that document the foraging strategies of storm petrels, which broadens our view on the range of behaviours displayed by pelagic seabirds.

CHAPTER 4

CHARACTERIZATION OF AN EXTINCT SEABIRD COLONY ON THE ISLAND OF SANTA LUZIA (CABO VERDE) AND ITS POTENTIAL FOR FUTURE RECOLONIZATIONS

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4.1. ABSTRACT

Islands worldwide have suffered seabird extinctions after the arrival of humans and the alien species they introduced. On Santa Luzia (Cabo Verde), an uninhabited island of 35 km^2, the presence of an impressive quantity of petrel bones in coastal dunes suggested the previous existence of an important seabird colony. Yet, these remains had not been identified and no seabird extinctions have been reported for the island. This paper characterizes the extinct seabird colony of Santa Luzia and discusses the chronology and possible causes of its demise. A total of 130 grid points in a 5 km^2 area and 38 supplementary points within and outside the main study area were excavated to collect bone remains. A total of 1318 anatomical elements, identified as White-faced Storm Petrel *Pelagodroma marina eadesorum* (85.3% of the minimum number of individuals, MNI), Boyd's Shearwater *Puffinus lherminieri boydi* (11.8% MNI) and Cape Verde Storm Petrel *Hydrobates jabejabe* (2.9% MNI), were found in 18% of the sampling points, within 1.25 km^2. Neither of the two former species currently breeds on Santa Luzia. In addition, two bones of the Cape Verde Shearwater *Calonectris edwardsii* and *Pterodroma* sp. were detected in the supplementary points. Radiocarbon dating of White-faced Storm Petrel (n = 10) and Boyd's Shearwater bones (n = 13) suggests that the colony probably went extinct during the first half of the twentieth century. The recent extinction of these species on Santa Luzia might be consequent on the arrival of humans and their domestic animals on the island. We estimate that the extinct seabird populations must have been at least hundreds of thousand strong, far larger than current

populations of the same species in Cabo Verde. We suggest that, following feral cat eradication, Santa Luzia has a significant potential for seabird restoration.

4.2. INTRODUCTION

Over the last centuries, largely following the Polynesian expansion and later European expeditions, many seabird species have suffered from population declines or been lost completely (Steadman, 2006). Islands worldwide often accommodate large seabird colonies (Belopol'skii, 1957; Croxall & Prince, 1980; Hunter et al., 1982; Pearson, 1968), and palaeornithological studies suggest that the majority of seabird extinctions have occurred in insular ecosystems (Olson & James, 1982; Quammen, 1996; Rando & Alcover, 2008,2010; Steadman, 2006; Worthy & Holdaway, 2002). Seabirds are particularly vulnerable to human-induced alterations, such as habitat destruction, hunting and introduced predators (Croxall et al., 2012; Dias et al., 2019). The loss of seabird species during the Holocene has involved more than 20 documented extinctions on islands around the world (Scofield, 2009; Steadman, 2006; Tyrberg, 2009), with many more probably having gone unnoticed. All these insular declines and extinctions seem to have been associated with the arrival of humans and subsequent alterations (Blackburn et al., 2004; Croxall et al., 2012).

Seabird fossils and subfossils are an important but poorly exploited resource, useful for understanding the long-term history of populations and communities, and the interpretation of biogeographical patterns and structure of modern-day communities. Fossils can provide information on co-occurring species during a specific period of time and in a specific area (Steadman, 2006; Steadman & Olson, 1985; Warheit, 2002), on the original species composition of a region, and may also contribute to a broader understanding of past environments and ecological interactions (Steadman, 2006). Fossil assemblages of extinct birds can also guide local actions to restore ecosystem function and processes through reintroductions (Barnosky et al., 2017; Wood et al., 2017).

Macaronesia is a group of five archipelagos of the northeastern Atlantic Ocean—Cabo Verde, the Canary Islands, Selvagens, Madeira and the Azores—where similar seabird assemblages are found (Monteiro et al., 1996a). Several seabird fossils from these archipelagos have been documented (Alcover & McMinn, 1995; Monteiro et al., 1996a; Pieper, 1985; Rando & Alcover 2008, 2010), but only one study referred to Cabo Verde, on the island of Sal (Boessneck & Kinzelbach, 1993). On the Canary Islands, the fossil record indicates that a significant part of the original community of Procellariiformes has disappeared, with three species confirmed extinct so far (McMinn et al., 1990; Rando, 2002; Rando & Alcover 2008, 2010; Walker et al., 1990).

Radiocarbon dating of extracted collagen of two extinct seabirds from the Canary Islands has allowed to establish an approximate date for their extinctions. One of these extinctions was probably associated with the arrival of aboriginal populations to the islands, and the other happened in the fourteenth century, coinciding with the arrival of Europeans (Rando & Alcover 2008, 2010).

Over the last 500 years, the native wildlife of the Cabo Verde archipelago suffered major declines and some extinctions, with seabirds being no exception (Hazevoet, 1995). Cabo Verde is currently home to eight species of breeding seabirds, three of which are endemic (Hazevoet, 2001; Semedo et al., 2020). Humans have exploited these populations for centuries, leading to drastic declines. The main colonies today exist only in largely inaccessible areas and it is likely that present seabird populations in Cabo Verde are mere remnants of much richer ones, both in diversity and numbers (Hazevoet, 2001; Semedo et al., 2020).

The island of Santa Luzia, situated in the north of the Cabo Verde archipelago, presents an extensive area of dunes where many unidentified seabird subfossils are partially buried (e.g. Mateo, 2012), suggesting the past existence of an important seabird colony. At the moment, only one species of seabird occurs on the island, the Cape Verde Storm Petrel *Hydrobates jabejabe* (Olivera et al., 2013).

The Cabo Verde Islands were colonized by the Portuguese in 1462 (Costa, 1939; Verlinden, 1963). Although uninhabited in the present day, Santa Luzia has seen human activity since the early fifteenth century and remained sparsely populated until the second half of the nineteenth century (Costa, 1939; Mateo, 2012). Along with the attempts of colonization came other alien mammals, such as dogs *Canis familiaris*, goats *Capra hircus*, domestic cats *Felis catus* and the house mouse *Mus musculus*, probably introduced to Santa Luzia when the first herdsmen settled there, during the eighteenth century. Until the mid-1960s, Santa Luzia was sporadically inhabited by shepherds and goat herders and temporarily visited by fishermen from neighboring islands (Bebiano, 1932; Diniz & Matos, 1994).

This paper aims to present the first detailed description of the current distribution of the seabird subfossil remains on Santa Luzia, the species composition and to estimate the likely period of extinction using radiocarbon dating. These data are used to discuss the likely causes of extinction and the relevance of deploying efforts to restore this island for breeding seabirds.

4.3. METHODS

4.3.1 STUDY SITE AND SAMPLING

The island of Santa Luzia (16°45′41″N, 24°45′38″W) has an approximate area of 35 km^2 (Fig. 4.1). The climate is desertlike and the vegetation is sparse. The island is characterized by stony plains, sand dunes and small mountain massifs (maximum altitude is 395 m).

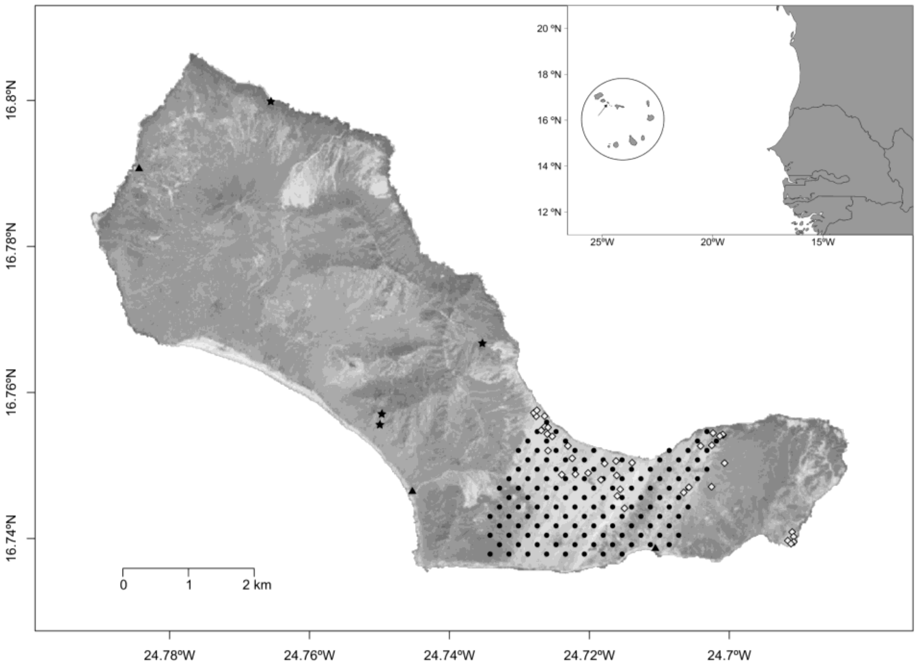


Fig. 4.1 Map of Santa Luzia. Inset: the position of Santa Luzia within Cabo Verde Islands. Circles represent study points sampled within a pre-defined grid and diamonds represent the supplementary sampling points within and outside the study area. Stars represent the probable nesting sites of Cape Verde Storm Petrel on Santa Luzia. Fishermen camps are represented with a black triangle

Fieldwork was carried out in September 2018. The study area was selected based on preliminary field observations, where abundant seabird bones are present. The selected study area consists of a clearly delimited area of mobile dunes, with sandy sediments of predominantly marine origin carried by the prevailing trade winds, plus a buffer zone of ca. 100–150 m (Fig. 4.1). The total area covers approximately 5 km^2. To carry out a systematic survey over the study area, we defined a regular (diagonal) grid comprising 130 points separated from each other by 200 m, marked with a handheld GPS. At each sampling point, a quadrat of 1 m^2 was set on the ground and all bone remains were collected by hand at the surface level, and carefully stored in plastic containers filled with soft cotton, until analysis. Anatomical elements that were broken beyond recognition were discarded. Wherever bones were present at the surface, we carefully dug 15 cm deep into the sediment to prospect for the presence of more sub-fossils in deeper layers, but none were ever found.

Bones were identified using the osteological reference collection at the Archaeosciences Laboratory (LARC, Ministry of Culture, Portugal), and the vertebrates' collection of the Department of Geology, Edaphology and Animal Biology of La Laguna University (DZUL). We also used our own reference collection prepared from bones of seabird species present on the island of Selvagem Grande, Madeira. We identified the laterality of the anatomical elements and quantified each anatomical element for each species at every sampling point. We then identified the first and second most frequent anatomical element for each species encountered over the entire study area for estimates of species abundance. To prevent overestimation of the number of individuals, ribs, vertebrae and phalanges were not included in the analysis. Species abundance was quantified based on the Number of Identified Specimens (NISP), where specimens refers to anatomical elements, with the Minimum Number of Individuals (MNI) of each species estimated as the number of the most frequently observed bone type of a given laterality.

Estimates of the number of adult birds of each species for the entire area were determined as the mean of the MNI (or NISP, in items per m^2) obtained at all sampling points, and then multiplied by the total studied area. To establish confidence intervals for the estimated parameters, we used a bootstrap procedure (Efron & Gong, 1983), resampling the number of bones found in each square 10,000 times (with replacement). The 95% confidence intervals were calculated by the percentile method, i.e., by selecting the

2.5 and 97.5% quantiles of the average number of bones obtained in each bootstrap iteration (Crowley, 1992). All analyses were conducted in the R 3.5.0 environment (R Core Team, 2020).

In addition to the grid sampling, we also carried out a series of supplementary sampling points within and outside the study area to check for the presence of additional species represented in the subfossils and to detect any additional areas with significant bone deposits. Counts from these supplementary points were not included in the estimation of NISP or MNI for the area (see supplementary material Annex C, Table C1).

Many bones of seabird nestlings were also present in the study area but only the bones of adult birds were considered. The bones of chicks can be easily identified since they are smaller in size and are not yet ossified in their proximal and distal epiphyses. The latter phenomenon makes it impossible to determine the laterality of the anatomical elements and to identify them. Additionally, they are often more fragile and suffer more fragmentation.

4.3.1 RADIOCARBON DATING

Thirteen humeri of Boyd's Shearwater *Puffinus lherminieri boydi* and ten tibiotarsi of White-faced Storm Petrel *Pelagodroma marina eadesorum* were selected for radiocarbon analysis to estimate their age. The collagen of the bones was extracted and directly dated for radiocarbon (^{14}C) by accelerator mass spectrometry (AMS) at the at the Keck Carbon Cycle AMS Laboratory at the University of California, Irvine, using standard procedures (Brownet al., 1988; Longin, 1971).

Radiocarbon samples from species that obtain their carbon from a source (or reservoir) different from atmosphericcarbon, such as seabirds, will yield radiocarbon dates that are overestimated by about 400 radiocarbon years compared to a bone from a terrestrial ecosystem (Stuiver & Braziunas, 1993). Therefore, a reservoir correction mustbe made to any conventional marine dates to account for this difference.

Radiocarbon data were calibrated using the program OxCal 4.4 (Bronk Ramsey, 2009), the marine calibration curve Marine20 (Heaton et al., 2020) with a regional correction, or ΔR, of 70 ± 70, obtained from marine samples (mollusk shells) and terrestrial samples (goat bones) from São Vicente Island, Cabo Verde Archipelago (Monge Soares et al., 2011). Calibrated calendar ages derived from the radiometric results are reported here as years CE (Current Era). Calibrated radiocarbon dates are expressed as 2σ intervals (i.e., $P = 95.45\%$) indicating that the true age of the dated material is more recent than the lower limit value of the 2σ interval and independently, it is older than the upper limit value of the 2σ interval (e.g., Ramis et al., 2002; Rando & Alcover, 2008; Zilhão, 2001). That is, if the calibrated age of a sample is 644–1010 CE, the true age of the sample is more recent than the year 644 CE but older than the year 1010 CE with a probability of 95.45%.

We applied an optimal linear estimation method (Clements et al., 2013; Roberts & Solow, 2003; Solow, 2005) to the lower limits of the 2σ intervals obtained from calibration, using these data like sighting records to approach, in a conservative way, to the extinction year of the bird colony. Confidence intervals (i.e., 95% CI) were calculated using R 3.5.0 (R Core Team, 2020) and the package "sExtinct" (Clements, 2013).

In addition, we used the Bayesian radiocarbon calibration software BCal (Buck et al., 1999; Buck & Bard, 2007) to calculate the probability that a given year is contained between the lower and upper temporal bounds of the dated samples.

4.4. RESULTS

4.4.1 TAXONOMIC COMPOSITION OF THE SEABIRD ASSEMBLAGE

All sub-fossils were found on the surface of the dunes, with no further remains being found after digging into the sediment (Fig. 4.2). We found no visible stratigraphy. Of the 130 quadrats sampled, 10 (8%) contained seabird bones and 21 (16%) had fragments of eggshells (Fig. 4.3). A total of 407 bone remains were collected and examined, resulting in at least 136 individuals of three species of Procellariiformes: White-faced Storm Petrel, Boyd's Shearwater and Cape Verde Storm Petrel *Hydrobates jabejabe*. White-faced Storm Petrel was the most abundant and widespread seabird in the assemblage, with a MNI of 116, estimated from tarsometatarsi and tibiotarsi. Boyd's Shearwater was also well distributed but found in lower numbers (Fig. 4.3, Table 4.1), with a MNI of 16 and Cape Verde Storm Petrel was represented by 4 bones, each corresponding to a different individual (Fig. 4.3, Table 4.1).

The estimated number of adult birds represented in bone remains for the study area was 4,600,000 (95% CI 1,720,000–8,200,000) for White-faced Storm Petrel, 640,000 (95% CI 200,000–1,200,000) for Boyd's Shearwater and 160,000 (95% CI 0–440,000) for Cape Verde Storm Petrel.

The supplementary sampling points provided two bones of both Cape Verde Shearwater *Calonectris edwardsii* and a gadfly petrel *Pterodroma* sp. (MNI = 1 in each case). The latter bones probably correspond to Cape Verde Petrel *Pterodroma feae*, but the small sample prevented their identification with full confidence.

In addition to seabird remains, we also found three mandibles of the extinct Cape Verde giant skink *Chioninia coctei* within the grid sampling.

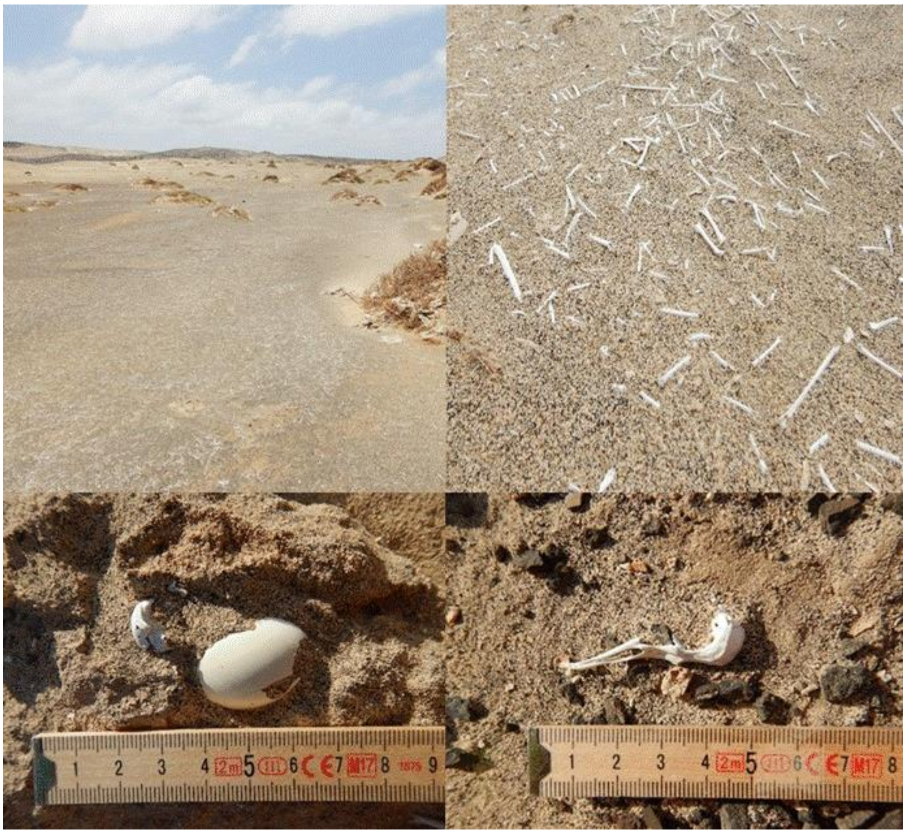
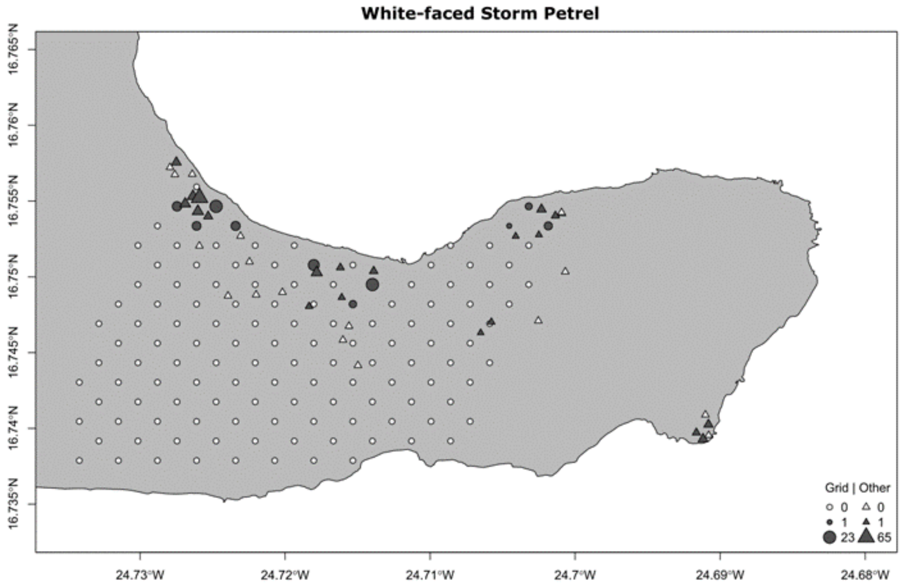
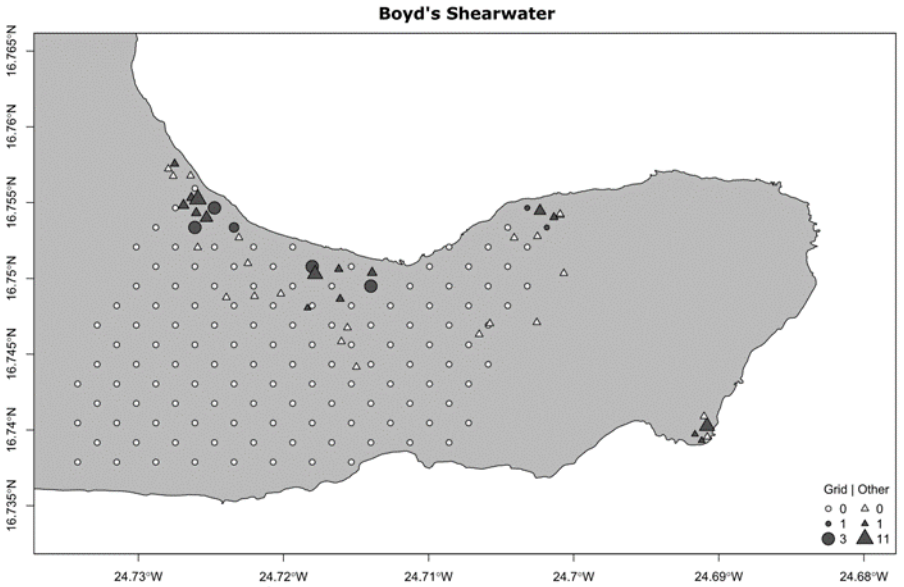


Fig. 4.2 Images of the seabird subfossils from dune deposits in Santa Luzia, Cabo Verde. Bottom: Egg and skull of White-faced Storm Petrel


White-faced Storm Petrel


Boyd's Shearwater

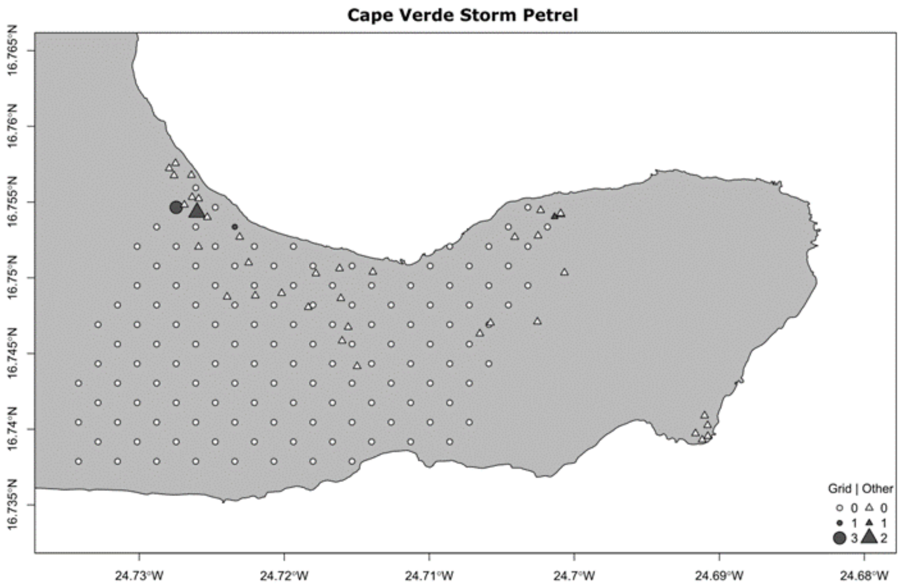

Cape Verde Storm Petrel

Fig. 4.3 Species abundance in terms of MNI (minimum numbers of individuals) of White-faced Storm Petrel, Boyd's Shearwater and Cape Verde Storm Petrel from the bird bone assemblage collected in the dunes of Santa Luzia, Cabo Verde. Circles represent study points sampled within a pre-defined grid and triangles represent the supplementary sampling points within and outside the study area

4.4.2 RADIOCARBON DATING

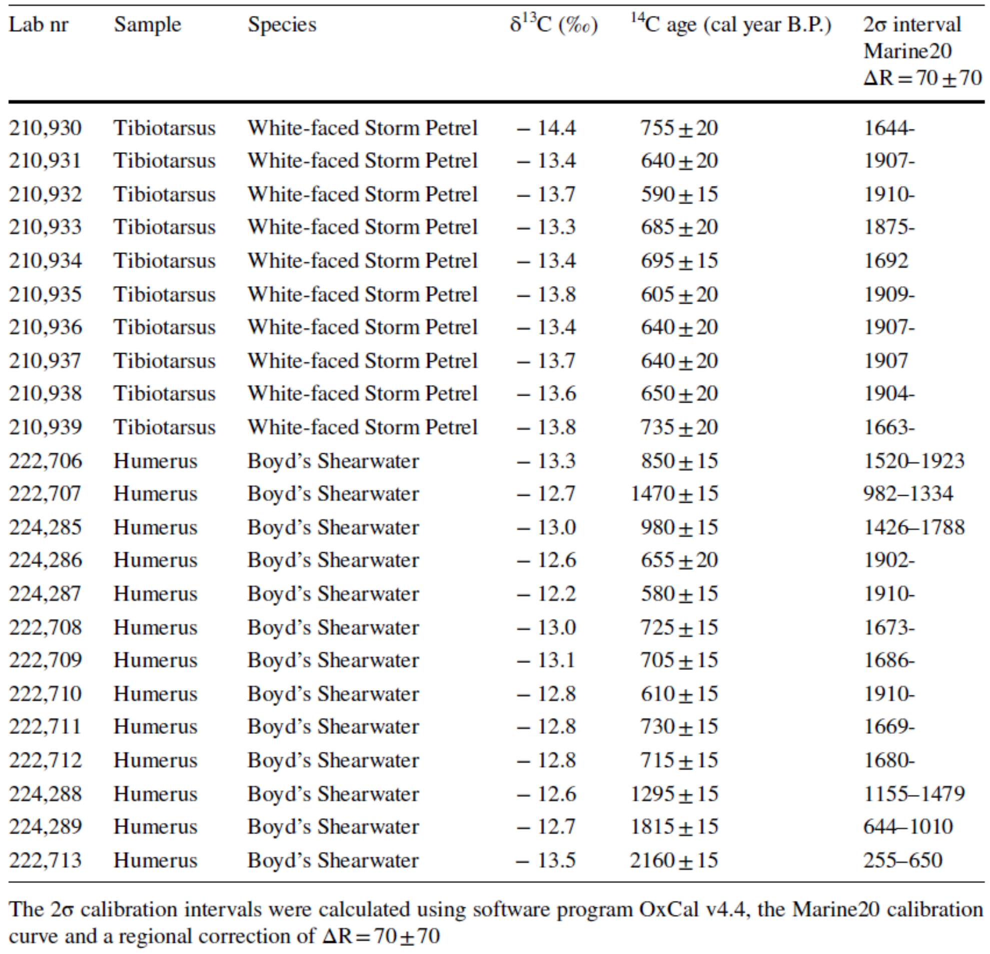
Calibrated ages are shown in Table 4.2 (and supplementary material Fig. C1). Most dates fell insidethe II millennium CE, only two samples (224,289 and 222,713) showed both limits of 2σ calibration interval in the I millennium. In all the samples of White-faced Storm Petrel and seven of the samples of Boyd's Shearwater the upper limits of the 2σ calibration interval extended out the calibration range. In addition, the lower limit of the 2σ interval of nine of these samples fell inside the twentieth century, showing a recent extinction event for the colony. The estimated extinction year for the seabird colony was 1911, with a confidence interval 1910–1934 (95% confidence). Due to the fact that we used the lower limits of the 2σ interval to retrieve this estimate, the extinction of the colony almost certainly occurred after 1911. In addition, the analysis performed using BCal shows that the probability for year 1934 to be contained between the lower and upper temporal bounds of the dated samples (Table 4.2) was 0.78, strongly suggesting that the seabird colony was still present during this year.

Table 4.1 Species abundance in terms of NISP (number of identified specimens) and MNI (minimum numbers of individuals) of each identified species from the bird bone assemblage collected from the bird bone assemblage collected from the Santa Luzia dunes

Species	NISP	Most abundant anatomic element (NISP)	2nd most abundant anatomic element (NISP)	MNI	MNI per point of occurrence (mean ± SD; range; *N*)	FO (%) (*n* = 130 plots)	NF (%) (MNI total = 136)
White-faced Storm Petrel	378	Tarsometatarsus (234)	Tibiotarsus (144)	116	11.6 ± 7.40 (1–23; 10)	7.7	85.3
Boyd's Shearwater	25	Humerus (22)	Tibiotarsus (3)	16	2.3 ± 0.95 (1–3; 7)	5.4	11.8
Cape Verde Storm Petrel	7	Humerus (5)	Tarsometatarsus (2)	4	2.0 ± 1.41 (1–3; 2)	1.5	2.9

The frequency of occurrence (FO) is represented by the number of points in which a specific seabird species was found in relation to the total number of points. Numeric frequency (NF) is represented by the number of individuals of a species in relation to the total number of individuals

Table 4.2 Radiocarbon age (cal year B.P.—Before Present) and 2σ calibration intervals (calibrated years *Current Era*-CE) of White-faced Storm Petrel and Boyd's Shearwater bones of Santa Luzia island



Lab nr	Sample	Species	$\delta^{13}C$ (‰)	^{14}C age (cal year B.P.)	2σ interval Marine20 ΔR = 70 ± 70
210,930	Tibiotarsus	White-faced Storm Petrel	− 14.4	755 ± 20	1644-
210,931	Tibiotarsus	White-faced Storm Petrel	− 13.4	640 ± 20	1907-
210,932	Tibiotarsus	White-faced Storm Petrel	− 13.7	590 ± 15	1910-
210,933	Tibiotarsus	White-faced Storm Petrel	− 13.3	685 ± 20	1875-
210,934	Tibiotarsus	White-faced Storm Petrel	− 13.4	695 ± 15	1692
210,935	Tibiotarsus	White-faced Storm Petrel	− 13.8	605 ± 20	1909-
210,936	Tibiotarsus	White-faced Storm Petrel	− 13.4	640 ± 20	1907-
210,937	Tibiotarsus	White-faced Storm Petrel	− 13.7	640 ± 20	1907
210,938	Tibiotarsus	White-faced Storm Petrel	− 13.6	650 ± 20	1904-
210,939	Tibiotarsus	White-faced Storm Petrel	− 13.8	735 ± 20	1663-
222,706	Humerus	Boyd's Shearwater	− 13.3	850 ± 15	1520–1923
222,707	Humerus	Boyd's Shearwater	− 12.7	1470 ± 15	982–1334
224,285	Humerus	Boyd's Shearwater	− 13.0	980 ± 15	1426–1788
224,286	Humerus	Boyd's Shearwater	− 12.6	655 ± 20	1902-
224,287	Humerus	Boyd's Shearwater	− 12.2	580 ± 15	1910-
222,708	Humerus	Boyd's Shearwater	− 13.0	725 ± 15	1673-
222,709	Humerus	Boyd's Shearwater	− 13.1	705 ± 15	1686-
222,710	Humerus	Boyd's Shearwater	− 12.8	610 ± 15	1910-
222,711	Humerus	Boyd's Shearwater	− 12.8	730 ± 15	1669-
222,712	Humerus	Boyd's Shearwater	− 12.8	715 ± 15	1680-
224,288	Humerus	Boyd's Shearwater	− 12.6	1295 ± 15	1155–1479
224,289	Humerus	Boyd's Shearwater	− 12.7	1815 ± 15	644–1010
222,713	Humerus	Boyd's Shearwater	− 13.5	2160 ± 15	255–650

The 2σ calibration intervals were calculated using software program OxCal v4.4, the Marine20 calibration curve and a regional correction of ΔR = 70 ± 70

4.5. DISCUSSION

Our results provide the first insights into the extinct seabird populations of the island of Santa Luzia, Cabo Verde. The seabird remains found at the sampling area consisted of bones in the order of millions of individuals and represented five seabird species: White-faced Storm Petrel, Boyd's Shearwater, Cape Verde Storm Petrel, Cape Verde Shearwater and *Pterodroma* sp. The lower limits of 2σ interval of several samples (Table 4.2 and supplementary material, Fig. C1) provide evidence that this seabird colony persisted on the island at least until the beginning of the twentieth century. Elderly members of the local communities whom we interviewed, some of whom grew up on

Santa Luzia, have no memory of seabirds on the island, supporting the idea that the extinctions happened before the mid-twentieth century.

The island of Santa Luzia was probably an important nesting locality for these species, especially for the White-faced Storm Petrel, given the very large estimated number of individuals. Our estimation of 4.6 million individuals encompasses at least three centuries of existence, which represents at least 15,000 birds dying per year. We can briefly speculate on the possible size of the colony, taking into account the individuals found within the study area (i.e.,not considering those found at the supplementary points). Assuming an annual adult mortality rate of 8% (e.g., Beck & Brown, 1972; Oro et al., 2005; Schreiber & Burger, 2001; Warham, 1996), and assuming that only a quarter of the mortality occurs at the colony (this is conservative, as very few small petrels are found dead in present-day colonies), 15,000 deaths per year would imply a living population at any moment of over 750,000 individuals. Many bones have probably by now been destroyed or washed away(most bones are relatively recent), so this estimate is likely conservative. Alternative simulations, with a progressively declining population due to cat predation give even higher estimates of the original population. Despite the massive uncertainties in these necessarily speculative calculations, there is little doubt that the colony at Santa Luzia was massive.

While the White-faced Storm Petrel is not currently present on Santa Luzia, it still breeds on Branco islet, ca. 10 km to the east (Hazevoet, 1995; Vasconcelos et al., 2015), on Rombo (near Brava) and Pássaros (Boavista) andLaje Branca (Maio) islets (Hazevoet, 2001; Semedo et al., 2020). Currently, the population of White-faced Storm Petrel in Cabo Verde is estimated at less than 10,000 pairs (Hazevoet, 2010), two orders of magnitude smaller than our tentative estimate of the extinct population of Santa Luzia. White-faced Storm Petrels nest mostly in flat areas with sandy soil where they can excavate their burrows (Del Hoyo et al., 1992). The population of White-faced Storm Petrels in Cabo Verde is particularly vulnerable due to the scarcity of available nesting habitat that is free of terrestrial introduced predators, further threatened by soil erosion, most likely limiting the size of the colonies of this species (all predator-free habitat is currently occupied). The small size and number of extant colonies make White-faced Storm Petrels extremely vulnerable to introduced predators and to anthropogenic threats such as disturbance by the trampling of burrows.

The extinct Boyd's Shearwater population, although possibly much smaller than that of the White-faced Storm Petrel, was still sizeable. For the same time period of 300 years, we found about one shearwater for every 10 White-faced Storm Petrels, and so the population might have consisted of tens of thousands of pairs. The current estimate of the population of this Cape Verde-endemic subspecies for the entire archipelago is ca. 5000 pairs (BirdLife International, 2018) and this species is thought to have bred on most of theislands and islets of Cabo Verde (Hazevoet, 1995; Semedo et al., 2020). Currently, the main colonies are located on Raso, Branco and Cima islets. Although Boyd's Shearwater may nest in burrows similar to those of the White-faced Storm Petrel, as they do on the islets of Rombo, the preferredbreeding habitat include crevices in cliffs and burrows underrocks, at different altitudes.

The Cape Verde Storm Petrel is endemic to Cabo Verde and is known to breed on the islets of Cima (one of the Rombo islets), Branco, Raso and possibly on the islets of Pássaros and Curral Velho, both off Boa Vista (Hazevoet, 1995) as well as along the coasts of some of the main islands(Hazevoet, 1994, 1995). Cape Verde Storm Petrels breed in crevices in cliff holes and burrows under rocks. However, on Cima, Branco and Pássaros islets they also nest in burrows among White-faced Storm Petrels (Semedo et al., 2020). In our study, the Cape Verde Storm Petrel was the species thatoccurred least frequently. However, it seems to be the only one of the three still breeding on Santa Luzia, with breedingrecords from a small area of inaccessible cliffs sites where they are likely protected from the population of cats on the island, which would otherwise likely drive them to extinction (Oliveira et al., 2013; Semedo et al., 2020). Moreover, thespecies also persists in some of the main inhabited islands with cats and rats, such as Santo Antão, probably in equallyinaccessible sites (Semedo et al., 2020). Despite the lack of census data, the restricted distribution of the current Cape Verde Storm Petrel population on Santa Luzia suggests thatit is only a small remnant of the one which once existed on this island.

The endemic Cape Verde Shearwater and possibly Cape Verde Petrel were found in the supplementary points, and we were not able to estimate the number of individuals. Cape Verde Shearwater has a wide distribution in the archipelago generally occurring near the coast at low-elevation areas, butat lower densities on populated islands (Semedo et al., 2020). For a long time (probably several centuries), the species hasbeen exploited by humans for food and bait, especially atits main breeding colonies (i.e., Raso and

Branso Islets). In contrast, Cape Verde Petrel occurs only on mountainous sites, from mid-to-high elevations, on Santo Antão, São Nicolau, Santiago and Fogo islands (Semedo et al., 2020). Cape Verde Petrels have been harvested by local people and predated by cats for centuries, threats which persist today. Indeed, a recent study on Fogo Island shows that this species was the bird most frequently consumed by feral cats (Medina et al., 2010).

At the time of the archipelago's colonization, the seabird colony on Santa Luzia was probably massive, as the subfossil remains indicate. However, our data suggest that these seabird populations went extinct in a relatively short period of time. In contrast, the populations on neighboring islands (Branco and Raso) persisted, suggesting that seabird extinctions on Santa Luzia were driven by threats occurring at the colony rather than at sea, as the latter would have affected neighboring colonies too.

On some islands and islets throughout the Cabo Verde archipelago, seabirds have become totally extinct due to the combined predation by humans and alien mammals (Hazevoet, 1994; Semedo et al., 2020). Due to the lack of natural resources and inclement conditions for agriculture on Cabo Verde (Caniato & Naurois, 2006), seabirds are known to have been hunted by settlers (de Naurois, 1969), resulting in the decline of seabird populations in the archipelago (Hazevoet, 1995; Murphy, 1924). Nonetheless, the seabird remains found in Santa Luzia showed no sign of poaching. On the most populated islands of Cabo Verde, seabirds are mainly found in areas almost inaccessible to humans (Semedo et al., 2020).

The effect of the introduction of alien mammals to oceanic island species is dramatic and well documented (e.g., Steadman, 2006; Worthy & Holdaway, 2002). The house mouse (*Mus musculus*) occurs on all inhabited islands of Cabo Verde, although there are no records on the presence of this species on the uninhabited islands, except on Santa Luzia Island (Hazevoet & Masseti, 2011; Semedo et al., 2020) and Rombo islets (Semedo et al., 2020). Currently, house mice have a widespread distribution but a low abundance on Santa Luzia Island, appearing to be particularly associated with fishermen camps (Geraldes et al., 2016). Although general abundance on the island is low, house mice densities show fluctuations and may be very high at times (unpublished data). In general, house mice are not considered as an important threat to seabirds (Angel et al., 2009; Burger & Gochfeld, 1994; Campos & Granadeiro, 1999; Dias et al., 2019) despite notable exceptions (Jones et al., 2019), and are unlikely to have been the cause of the demise of seabirds on Santa Luzia.

Examples of seabird extinctions caused directly by goats are scarce. However, goats are known to impact burrowing petrels, due to the depletion of vegetation cover and subsequent soil erosion (Bell, 1995). In Cabo Verde, the presence of goats altered the natural habitat of Grande Islet, the largest of the Rombo Islets, known for housing large colonies of seabirds in the past (Murphy, 1924). Goats are no longer present on Santa Luzia Island.

Domestic cats are one of the major threats to seabirds throughout the world (Burger & Gochfeld, 1994; Medina et al., 2011; Moors & Atkinson, 1984), even when other invasive species are present (Courchamp et al., 2003, Hervías et al., 2013). On Santa Luzia, this invasive predator is considered as one of the main threats to native endangered species, as such, it is likely that cats played a decisive role in the extinction of seabirds on Santa Luzia, which is also supported by their present predatory role which forces the confinement of Cape Verde Storm Petrel to inaccessible places on this island (Oliveira et al., 2013).

In the recent past, other local extinctions have occurred on Santa Luzia, such as the endemic Cape Verde giant skink *Chioninia coctei* (Duméril & Bibron, 1839), declared extinct at the beginning of the twentieth century (Mateo, 2012; Schleich, 1996). The causes of its extinction may have included over-collection, and predation by feral cats (Andreone, 2000). This species was largely dependent on seabird colonies, feeding on eggs and chicks (Bocage, 1896; Mateo, 2012), and the disappearance of these seabird colonies may also have contributed to its extinction. Recently, Medina et al. (2020) showed that on Santa Luzia, feral cats have also turned out to be a serious threat to reptiles, which represent more than 70% of their diet (in terms of consumed biomass).

During the last few years, a program for the eradication of feral cats has been implemented on Santa Luzia Island. To date, a total of 131 feral cats have already been eliminated, leading to a current population estimate close to zero (Martinez et al., 2021). By removing the threat of the invasive species, efforts to re-establish extirpated species can be undertaken (Bellingham et al., 2012; Kappes & Jones, 2014), such as for the critically endangered Raso lark, *Alauda razae* recently re-established on Santa Luzia by a translocation program (Brooke et al., 2020). The feral cat eradication program appears to be producing good results for the native species, such as the Bar-tailed Lark *Ammomanes cinctura*, the Cream-colored Courser *Cursorius cursor* and, the Common Quail *Coturnix coturnix* which are now common throughout the island (contrasting with their rarity at the beginning of the project) (BirdLife International, 2020). Also, the terrestrial herpetofauna (geckos and skinks) appears to have increased and many juveniles are regularly observed throughout the island (Brooke et al., 2020).

Santa Luzia is the largest island in the Marine Protected Area (MPA) composed of three islands (Santa Luzia, Raso and Branco) and the surrounding sea, and it has the greatest potential to provide significant additional habitat for seabird species (Geraldes et al., 2016). The sub-fossil evidence in this study confirmed the presence of several seabird species in the past, several of which still nest on nearby islands (Geraldes et al., 2016; Semedo et al., 2020). After the eradication of cats, recolonization of Santa Luzia by seabirds could take place naturally or be assisted by reintroduction programs. Passive recovery of seabirds may not easily occur for islands > 25 km from source populations (Buxton et al., 2014; Kappes & Jones, 2014). Although, Santa Luzia is less than 8 km from potential source populations of seabirds, natural recolonizations are known to occur extremely slowly due to the philopatric character of many seabird species (Bellingham et al., 2010; Buxton et al., 2014). Further research should aim at improving our knowledge on potential breeding areas for seabirds on Santa Luzia and evaluating the seabird colonies on the nearby islands as possible source populations for future re-introduction projects. This action will only be possible if the complete removal of feral cats from the island is successful. Consistent and effective monitoring plans should be an integral component of a future seabird restoration project on Santa Luzia.

4.6. CONCLUSION

In conclusion, our study demonstrates that Santa Luzia was once an important nesting site for three seabird species, especially for White-faced Storm Petrel. In the past, Santa Luzia may have hosted the largest White-faced Storm Petrel and Boyd’s Shearwater colonies in the entire Cabo Verde archipelago. The introduction of alien species, particularly cats, together with direct human predation and disturbance arising from the colonization of Santa Luzia are the likely drivers of the extinction of this seabird colony. The nearest islets of Raso and Branco — neither of which has ever been inhabited — still maintain important populations of seabirds, which is in support for our hypothesis. Santa Luzia has a great potential to provide significant additional habitat for these species, once the current threats are removed. The strong declines in feral cat numbers already lead to an increase in the number of birds detected while prospecting for nests (Cape Verde Shearwater calls regularly recorded and Boyd’s Shearwater detected in burrows on the ground) (unpublished data). The complete removal of cats would represent an important step to the recolonization of the island by the seabird species that once occurred there.

CHAPTER 5

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ARTIFICIAL NESTS AS A TOOL FOR RESEARCH ON WHITE-FACED STORM PETREL ON SELVAGEM GRANDE, NORTHEAST ATLANTIC

Maria Alho

5.1. ABSTRACT

Burrow-nesting species, like storm petrels, are difficult to study and sample. In this study, carried out at in Selvagem Grande, Portugal during 2018 and 2019, we evaluate the effectiveness of artificial nests as a tool to study White-faced Storm Petrel during the breeding season and potentially also for conservation. We compared the breeding success of pairs nesting in artificial nests and in manipulated natural nests and also provide a description of some main aspects of the breeding biology of White-faced Storm Petrel. Artificial nests (N=42) were installed at pre-existing breeding burrows (i.e., artificial nests were set on deep natural burrows, where we installed a wooden chamber). Our results show very high occupancy rates (presence of an adult and egg or just an egg): 70% in the first year after the installation of the artificial nests and 83% in the two years after. Hatching success was higher in artificial nests than in natural nests, with values exceeding 70% in both breeding seasons. Overall, 15 of the 36 ringed White-faced Storm Petrels returned to the same nest (41.7%, natural or artificial) in the following breeding season. Seven out of 12 ringed birds returned to the same artificial nest (58.3%), and the corresponding return rate for natural nests was 25%. Temporary egg neglect, which seems to be a typical feature of this species, was also found in artificial nests. One of the major causes of hatching failure at natural nests was egg predation by Madeiran Wall Lizards *Teira dugesii*. The artificial nest model used in this study may be used for other storm petrels, facilitating less-intrusive future studies and conservation actions

5.2. INTRODUCTION

Our ability to study (e.g., track, count and sample) seabirds is key to understand their ecology and behaviour and assist in their conservation (Armstrong & Reynolds, 2012). Research on the breeding biology and habits during the breeding season of small Procellariiform species, particularly those that typically nest in relatively inaccessible burrows, like storm petrels, is particularly challenging and as a result, these species remain relatively understudied (Brooke, 2004a, Rodríguez et al., 2019).

Monitoring burrow-nesting seabirds can include a variety of more or less invasive procedures, depending on the data being collected (Fischer et al., 2018). In general, non-invasive methods that do not directly reveal the state of the nest, such as Radio Frequency Identification, remote cameras, or call-playback responses, are not well suited for long-term research on small seabirds (Fischer et al., 2017). Burrow-scopes or manually inspecting the burrow's contents are two common invasive methods used to inspect the nest chamber (Burger & Lawrence 2000). These methods appear to be more effective for some species than others (Parker & Rexer-Huber, 2016), nevertheless they are potential causes of disturbance (Blackmer et al., 2004). In studies requiring the capture of birds (e.g., tracking studies, biological sampling), altering the access and internal structure, by enlarging the entrance hole or opening a direct access to the nest chamber is a common procedure (Rayner et al., 2007). However, this technique may reduce the burrow's suitability in terms of temperature regulation, or facilitate the access for predators or competing burrow-nesting species, which may increase the likelihood of nest failure (Carey, 2009; Marks & Leasure, 1992). Moreover, this may cause habitat damage, collapse of burrows, flooding and increases the risk of disturbance or abandonment (Carey, 2009; Ryan et al., 2006; Warham, 1990; Wilson 1986).

Artificial nests have been successfully used as a research tool to study different burrowing seabird species, particularly for conservation purposes (Bolton et al., 2004; Gummer et al., 2015), including storm petrels (*Hydrobates leucorhous* Buxton & Jones, 2012; Podolsky & Kress, 1989, *Hydrobates pelagicus* Bolton, 1996; De León & Mínguez, 2003; Dell'Ariccia et al., 2015; Libois et al., 2012; Mariné & Bernard, 2020, *Hydrobates castro* Allan, 1962; Bolton et al., 2004, *Hydrobates furcatus* Buxton & Jones, 2012, *Pelagodroma marina* Rayner et al., 2017). Despite being an invasive approach (Miskelly et al., 2009; Priddel & Carlile, 1995; Warham, 1990), artificial nests provide easy access to the nest chambers, allowing researchers to conduct routine monitoring and manipulation of eggs, as well as capture, identify, and sample the adults or chicks, with a high temporal resolution (Lambrechts et al., 2010). Artificial nests have been constructed to reduce interspecific competition, increase existing breeding habitat, reduce the risk of predation and nest collapse, or establish new breeding locations through chick translocation (Lambrechts et al., 2010; Priddel & Carlile, 1995; Wilson, 1986). The method generally employed is to create artificial nests to act as additional burrows in order to increase nesting opportunities for birds. Such strategy has a major disadvantage related to the fact that it may take several breeding seasons for the birds to occupy the artificial nests (e.g., Bolton et al., 2004; Libois et al., 2012; Wilson, 1986). Also, most individuals who use artificial nests appear to be first-time breeders (Bourgeois et al., 2015), and this lack of experience is often linked to reduced reproductive success (Mougin et al., 2002; Wooller et al., 1990), which could be a source of bias in long-term surveys.

Providing artificial nests may also have negative consequences, resulting in increased ectoparasite infection (Fargallo et al., 2001), conspecific brood parasitism (Eadie et al., 1998), create unfavorable environmental variables inside brood chambers, resulting in a lower number of young fledged per nest (Mänd et al., 2005), and lower short-term survival of fledglings (Klein et al., 2007). Furthermore, artificial nests might have unanticipated consequences by acting as 'ecological traps' (Mänd et al. 2005, Klein et al. 2007) as they may allow supra-optimal breeding density or even enhancing predator attractiveness (Mänd et al. 2005; Sanz et al., 2003;).

The White-faced Storm Petrel *Pelagodroma marina* is a small burrow-nesting seabird (40–70 g; Marchant & Higgins, 1990) with a wide distribution range in the waters of the Atlantic, Pacific, and Indian Oceans (del Hoyo et al., 1992). An important fraction of the global population of the endemic European subspecies (*Pelagodroma marina hypoleuca*) is restricted to the Selvagens Islands, a small archipelago in the North-east Atlantic (Campos & Granadeiro, 1999; Silva et al., 2015). Birds first arrive at the colony in mid-December, eggs are laid from mid-March to early June, and the last chicks fledge in mid-August. A single egg is laid in the burrow, both parents incubate for an average of 54 days and the fledging period lasts an average of 60 days (Campos & Granadeiro, 1999).

During a study of White-faced Storm Petrels breeding on Selvagem Grande we used GPS devices to track their foraging movements during the breeding season (Alho et al., 2022). This required the daily monitoring of nests, which was carefully planned as storm petrels are particularly sensitive to handling at the nest (Carey, 2009). In this study, we began by modifying natural nests (digging a small hole above/parallel to the nest chamber of the natural nest) to have an easy access to the nest chamber. However, even with improved access to the burrow entrance, the risk of burrow collapse and subsequent disturbance/abandonment is still high (Carey, 2009; Warham, 1990; Wilson, 1986). For this reason, we installed artificial nests during the non-breeding season on pre-existing breeding cavities and assessed the efficacy of this technique in increasing the breeding performance of White-faced Storm Petrel. This method was devised to reduce the disturbance and collapse of the modified natural nests, enabling regular observation of the nest (without handling the birds as frequently). To ascertain whether this has any effect on breeding performance, we examine the breeding parameters and performance of White-faced Storm Petrels nesting in manipulated natural and artificial nests in two breeding seasons. Finally, we discuss factors affecting these breeding parameters in artificial nests in order to optimize their installation and to facilitate future long-term breeding and conservation studies of small burrowing petrels.

5.3. METHODS

5.3.1. STUDY AREA

We conducted fieldwork on the island of Selvagem Grande (30° 09′ N, 15° 52′ W), which is located in the North-east Atlantic, ca. 300 km south of the Island of Madeira (Portugal) and consists of a central flat plateau surrounded by cliffs. The sampling area was located in one of the two well-defined areas of sandy soil in the plateau where White-faced Storm Petrel breeds (Campos & Granadeiro, 1999). This area is situated on the central plateau of the island, south of the Tornozelos peak (Figure 5.1). Nests sites were selected on the periphery of the colony in order to avoid trampling and nest collapse and near a trail to facilitate monitoring and data collection.

5.3.2. FIELDWORK

Fieldwork was carried out in October 2017, between 28 March – 16 May, 20 June – 15 August and 1 - 17 October 2018 and between 1 April - 29 June 2019. Although we were absent from the island during the breeding season of 2020, the park-wardens of the Nature

Reserve checked the occupation of the artificial nests on the 5th June 2020, by which time it is expected that all eggs had been laid.

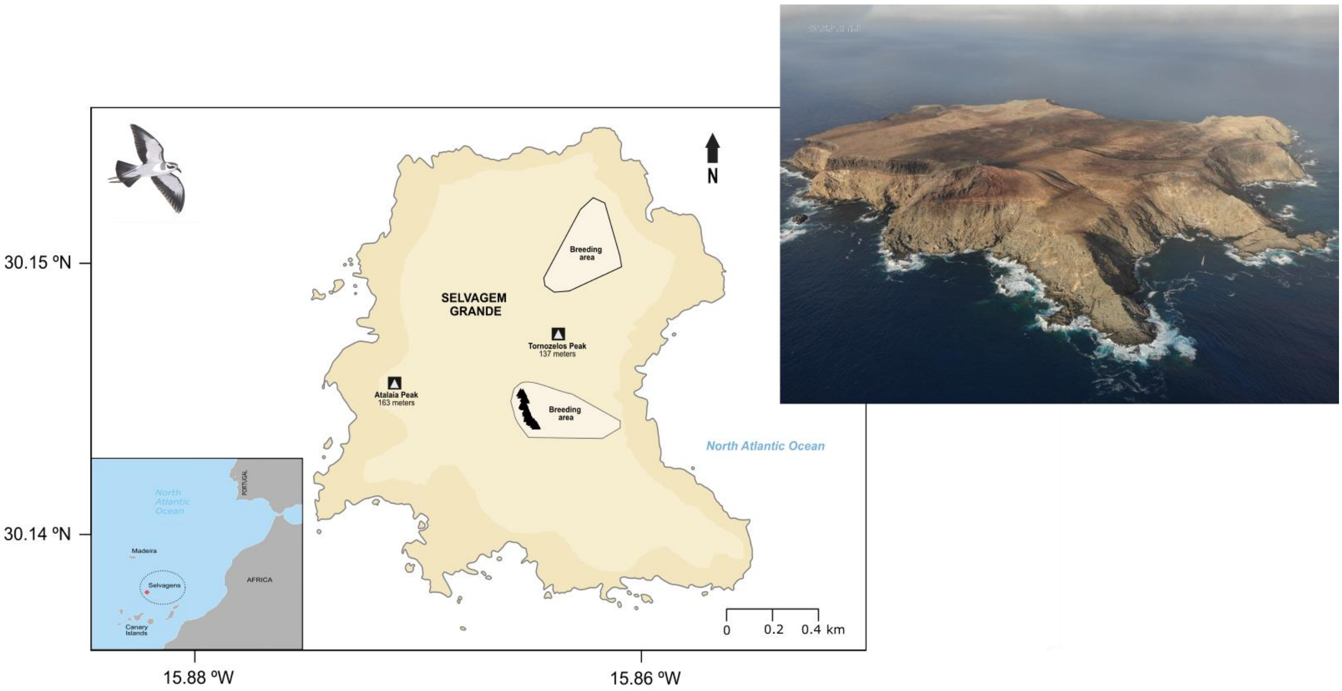


Fig. 5.1 Aerial photograph of the study area and the location of the breeding colony of White-faced Storm Petrel in Selvagem Grande and the distribution of the artificial nests, represented by black triangles (▲)

Manipulated natural nests

At the beginning of the 2018 and 2019 breeding seasons, a sample of 43 and 53 natural nests, respectively, were chosen and individually-marked for detailed studies (Fig. 5.2). The contents of natural nests (adult, egg or both) were checked by hand or with a borrowscope. Once nests were selected, we located the nest chamber and dug a small hole above it or on the lateral of it to access the nest chamber of each natural nest. These holes were covered with a flat stone or with a round plastic plant drip tray (secured with a stone Fig. 5.2). This setup facilitated access to natural nests and allowed regular inspection of contents.

Fig. 5.2 Natural nests individually-marked with the access to the nest chamber covered with a round plastic plant drip trays secured with stones

Artificial nests

In October 2017 (i.e., during the non-breeding season), ten artificial nests were installed at existing White-faced Storm Petrel nests that had signs of occupation from that year. During the 2018 non-breeding season (October), an additional 33 artificial nests were buried in natural nests where there were already birds the previous year with confirmed breeding success. The nests were set up during the non-breeding season to avoid the risk of destroying occupied nests. The artificial nests were made of square walls of 10 mm width untreated plywood boards with a hole done in one of the walls, two square lids (internal and external), and a 400-500 mm in length plastic (polyethylene) drainage tube (86 mm in diameter) tube leading to the entrance of nest chambers (see Fig. 5.3). Without the plastic drainage tube, artificial nests with lids measured 200 mm long × 200 mm wide × 250 mm high, and had no base, so that birds breed on natural substrate. The artificial nest had two lids to provide additional protection of the nest chambers from any weather events or predation by gulls. The external lid was covered with a large flat rock. The cost of each artificial nest unit with plastic drainage tube was around 6 euros.

Any nest material present in the nest chamber of each natural nest was placed inside each artificial nest. The plastic drainage tube was always placed with the original curvature of each natural nest where the artificial nest was placed and with the entrance slightly inclined upwards. Some soil present in the nest site was added in the tunnel. Care was taken to leave the burrow/tunnel entrance looking as natural as possible, and in the same location as the original burrow entrance. All artificial nests were individually-marked and their locations were registered using a GPS device.

One of the artificial nests had disappeared when we arrived on the study area at the beginning of the 2019 breeding season, with a total of 42 boxes remaining that year. In 2020, one artificial nest was also not found by the park-wardens of the Nature Reserve.

Fig. 5.3 Artificial nests of White-faced Storm Petrels from Selvagem Grande. Artificial nests installed in the field **(a,b,d)**. Material used to build the artificial nest **(c)**. Details of the internal and external lid **(f)**. Individual identification of the artificial nest **(e)**. Adult of White-faced Storm Petrel **(g)** inside the artificial nest cavity with egg and a chick of the same species **(h)**. Photos: Maria Alho

Breeding parameters

In order to identify the breeding pairs, one member of the incubating pair was marked with white paint on the forehead to facilitate identification of the two individuals from each other, in both natural and artificial nests without further manipulation. We only considered birds as a breeding pair when there was an egg in the nest. In this study, the following breeding parameters were estimated in natural and artificial nests: occupancy rate (proportion of nests where we recorded the presence of birds and/or eggs), laying rate (proportion of nests where an egg was found), hatching success (proportion of eggs that hatched), fledging success (proportion of hatched chicks which survived to fledging) and breeding success (proportion of eggs laid that resulted in a fledgling). Occupancy was only analyzed for the artificial nests as all of the natural nests monitored in this study were selected based on the presence of signs of occupation. Fledging was assumed to have been successful when burrows were found empty for two consecutive days (at the time that fledging occurs for each nest) and there were no signs of predation.

Natural nests were visited approximately every 1-3 days in 2018 and 1-5 days in 2019, and checked daily when we found an unattended egg until a parent had returned. Artificial nests were examined daily throughout incubation to determine laying dates, egg neglect rates and hatching dates. All nests were visited during daylight hours. The mean laying and hatching dates, and thus the incubation period, could not be determined in natural nests because they were chosen based on occupancy, and we were unable to inspect natural nests throughout the period of 27 May - 28 June 2019. All individuals who occupied artificial nests were ringed at the end of the 2018 and 2019 breeding season, as opposed to natural nests, where only the birds tracked using GPS were ringed. Return rates to the same nest was analyzed based on the individuals ringed in the 2018 breeding season as part of the mentioned study above (N = 12 birds from artificial nests; N = 24 birds from natural nests). Nests with egg neglect were recorded for all artificial nests. These periods of egg neglect were confirmed by the absence of an adult in nest chambers during nest checks. Natural and artificial nests that were occupied by other seabird species were also registered. Causes of nest failure (e.g., egg predation) were investigated and recorded whenever possible. Hatching and fledging success was compared between natural and artificial nests using Chi-square tests. Data are expressed as means ± standard deviations. All tests are two-tailed.

5.4. RESULTS

In total, 95 natural and 42 artificial White-faced Storm Petrel nests were monitored in the current study during the 2018-2020 breeding seasons. In 2018, artificial and natural nests showed a similar fledging success, with 21 of 23 eggs that hatched in natural nests and the 6 of the 6 eggs that hatched in artificial nests fledging successfully (χ^2= 0.56, P = 0.45; Table 1). However, hatching success was significantly higher in artificial than in natural nests in 2019 (χ^2= 12.8, P = 0.0004) and marginally higher in artificial nests in 2018 breeding season (χ^2= 3.9, P = 0.049). Both the occupancy rate and laying rate of artificial nests increased from 2018 to 2019. In 2020, both occupancy and laying rate in the artificial nests were similar to 2019 (Table 5.1).

Table 5.1 Breeding parameters of White-faced Storm Petrels nesting in natural and artificial nest sites on Selvagem Grande, Portugal, during the 2018-2020 breeding seasons

	2018		**2019**		**2020**
	Natural nest (n = 53)	Artificial nest (n = 10)	Natural nest (n = 46)	Artificial nest (n = 42)	Artificial nest (n = 41)
Occupancy rate	[a]	70%	[a]	83%	83%
Laying rate	[a]	60%	[a]	81%	83%
Hatching success	46%	100%	50%	71.4%	[b]
Fledging success	91.3%	100%	[b]	[b]	[b]
Breeding success	42%	100%	[b]	[b]	[b]

[a] Not calculated, as all of the monitored natural nests were selected based on the presence of signs of occupation (egg or adult).

[b] Not calculated, as fieldwork ended before the necessary information was obtained to calculate breeding parameters for some nests.

For artificial nests, there was a significant difference in mean laying dates between 2018 (8 April ± 7.7 days; N = 6; range: 1 April – 22 April) and 2019 (21 April ±11.3 days; N = 29; range: 9 April – 13 May) (Welch's t test, t = − 3.3073, df = 10.1, P = 0.008). The incubation period took 50.2 ± 4.5 days (N = 18; range: 44-66) and the mean hatching date was 6 June (± 9.9 days; N = 19; range: 28 May – 28 June) in the 2019 breeding season.

In 2018, 4 of the 7 (57.1%) occupied artificial nests had at least one egg neglect event, with 3 nests that had recordings of a second event (75%). During 2019, 18 of the 33 (54.5%) occupied artificial nests had at least one egg neglect event, with 10 nests recording a second event (55.6%). Eggs were neglected for periods that varied from one to four days in 2018 and one to ten days in 2019. On average, in 2018, the first egg neglect event occurred 12.5 days (± 4.6 days; N = 4; range: 7 – 18 days) after laying, and in 2019, it occurred at 3.9 days (± 1.9 days; N = 18; range: 1 – 8 days). The ten-day egg neglect event in 2019 occurred three days after laying. All the 4 eggs neglected in 2018 and 12 of the 18 eggs (66.7%) neglected in 2019, successfully hatched. In 2018, 4 (66.7%) of the 6 eggs that hatched in artificial nests were known to have been neglected at least once, while 12 (40%) of the 30 eggs that hatched in 2019 were known to have been neglected at least once. Occasionally, eggs of both types of nests were neglected for one or more days just before hatching and still survived.

Overall, 15 of the 36 ringed White-faced Storm Petrels (42%) returned to the same nest in the following breeding season. In 2019, out of the total number of birds ringed from artificial nests (N=12), seven returned to the same artificial nest (58%), two forming one pair. One individual returned to a nearby artificial nest where it had been nesting the year before. From the 24 birds ringed in natural nests in 2018, six individuals (25%) returned to the artificial nest buried where the natural nest in the previous year was. Additionally, one bird also dug the nest next to the artificial nest that was installed in 2018, matching the site of the natural nest where the individual breed. All the 15 individuals had bred successfully (all chicks fledged) in the previous year.

In natural nests, seven eggs in 2018 (14% of the total) and five eggs in 2019 (10.9%) were seen being predated by Madeiran Wall Lizards *Teira dugesii* (when the eggs were neglected). We found no evidence of Madeiran Wall Lizard egg predation in artificial nests, with a significant difference in egg predation between artificial and natural nests for both breeding seasons (χ^2= 5.48, P = 0.019). Deserted eggs were found in five natural nests (10% of the total) in 2018 and in eight natural nests in 2019 (17.4%). Three cases of deserted eggs in artificial nests were reported (8.8%) in 2019, and in one of these, one of the members of the pair was found dead with signs of predation near its nest. There was no difference in the proportion of deserted eggs between natural and artificial nests for both years (χ^2= 0.99, P = 0.319). In contrast to the natural nests, where eight (16%) and nine (19.6%) eggs disappeared and no remains were found in 2018 and 2019, respectively, no eggs disappeared from the artificial nests in either of the two breeding seasons. Regarding the artificial nests, all chicks successfully fledged in 2018. In 2019, three chicks were found dead inside the artificial nest chamber and two chicks simply disappeared from the nest site, without any obvious signs of nest disturbance. In natural nests, two chicks (2018) and one chick (2019), were found dead inside the nest chamber. We were unable to confirm with certainty that the maximum number of dead chicks in 2019 in both nests was as presented in this study, as fieldwork ended before all chicks had fledged. In 2018 only, two natural nests collapsed during the incubation phase.

In the first breeding season, 7 of the 53 natural nests (13.2%) were occupied by Band-rumped Storm petrel *Hydrobates castro* after White-faced Storm Petrel hatching failure (n = 6) and after fledging failure (n = 1). Apart from two nests that were occupied in the middle of April and May by Band-rumped Storm petrel, the rest were occupied in the second half of June. In 2019, one natural nest was occupied by Band-rumped Storm petrel and another by Bulwer's petrel *Bulweria bulwerii*, both after hatching failure in the White-faced Storm Petrel nests. The same occurred with the artificial nests. The following year, in 2020, the same artificial nest occupied by Band-rumped Storm petrel in 2019 was occupied again by the same species (no individual identification as rings were not checked). Additionally, another artificial nest was occupied by a pair of Bulwer's petrels.

5.5. DISCUSSION

The installation of artificial nests represented an effective tool to facilitate monitoring of White-faced Storm Petrels and may potentially also be useful for conservation. The results of our study show that artificial nests installed at existing breeding nests were attractive for White-faced Storm Petrels breeding on the Selvagem Island, with an occupancy rate of 70% in the first breeding season, and 83% in the following two years (N=42). Hatching success was higher in artificial nests than in natural nests, with values exceeding 70% in both breeding seasons. Egg neglect was found in both natural and artificial nests, which seems to be a typical feature of the breeding behaviour of this species. Our results reveal that, predation on eggs and chicks by Madeiran Wall Lizards was lower in the artificial than in natural nests. This suggests that artificial nests in our study area may provide a higher level of protection than natural nests, mainly until hatching.

The occupation of artificial nests by seabirds can take several years before birds accept and use these nests (e.g., Bolton et al., 2004; Libois et al., 2012). Comparing our study to the few other studies using artificial nests in storm petrels —especially for the first year of occupation—we found a rate of occupancy that is particularly high (Bedolla-Guzmán et al., 2016; Bolton, 1996; Bolton et al., 2004; De León & Mínguez, 2003; Libois et al., 2012). For example, Libois et al. (2012) demonstrated that following the installation and successful occupation of *Hydrobates pelagicus* in artificial nests, seven years were required to reach an occupancy rate of >80%. The high occupancy rate observed in our study might be due to the installation of artificial nests in natural burrows with signs of previous occupation (Bourgeois et al., 2015; De León & Mínguez, 2003). This is also supported by our ringing data. For instance, we observed that six individuals that occupied artificial nests in 2019 had returned to the same location where the natural nest from the previous year was. Additionally, we also hypothesize that the odour of the nest material and the soil from previous occupied nests that covered the nest chamber might increase the probability of occupancy of the artificial nests, providing the olfactory signal needed by the birds to relocate the nest (Bonadonna et al., 2003; Buxton & Jones, 2012; Mínguez, 1997; O'Dwyer et al., 2008). The nest site fidelity may be higher than reported in this study, considering that only individuals who were GPS-tracked (and hence suffered from some disturbance) were ringed in the manipulated natural nests.

In the current study, the average laying date in artificial nests was significantly earlier in 2018 than in 2019. This may be due to the typical asynchronization of breeding within the colony in storm petrels (Warham, 1990), a breeding behaviour already reported on White-faced Storm petrel in Selvagem Grande (Campos & Granadeiro, 1999). Incubation in the artificial nests averaged 50.5 days and this is consistent with what has been found in the previous study by Campos & Granadeiro (1999) in natural nests of White-faced Storm Petrel in Selvagem Grande, i.e., 53.7 days. The hatching success in natural nests was 46% and 50% for the 2018 and 2019 breeding seasons, respectively, which is lower compared to the value obtained by Campos & Granadeiro (1999) for the same colony in 1995 (hatching success was 60.7%, N = 89). This may have occurred due to the constant disturbance of natural nests, especially in 2018, as most of the natural nests had to be monitored daily, and many birds even needed to be handled for other research studies that were occurring on the island at the time. However, hatching success in artificial nests was higher than in the manipulated natural nests, with values exceeding 70% in both breeding seasons. Although artificial nests were also periodically checked, there was perhaps less nest disturbance since manipulating the birds in an artificial nest took less time and present lower risk of collapsing than in a manipulated natural nest. Despite the fact that we only have data for one breeding season, there was no difference between the fledging success of the manipulated natural nests of our study (91.3%) and the values obtained for the same colony in 1995 (88.9%; N = 54; in Campos & Granadeiro 1999) (χ^2= 0.101, df = 1, P = 0.75). Notwithstanding the small sample size, the same pattern was also observed using artificial nests, with a 100% fledging success rate in 2018 (χ^2= 0.741, df = 1, P = 0.38).

For this species, egg neglect was already documented, with Underwood & Bunce (2004) reporting that at least 40% of eggs in natural nests were neglected (N = 50) for White-faced Storm Petrel breeding at Mud Islands, Australia. Also, Campos & Granadeiro (1999) demonstrated that 66.7% of the eggs that hatched (N = 54), had been neglected at least once. A similar pattern of results was obtained in our study for artificial nests during the 2018 breeding season (57.1%). Additionally, we found that White-faced Storm Petrel could tolerate 10 days of egg neglect in an artificial nest before the chick successfully fledged, which is the longest egg neglect time recorded for the species (Campos & Granadeiro, 1999 reported a maximum of 6 days in natural nests). Therefore, the recorded duration of incubation is probably significantly longer than the time needed for chick development, and differences in duration of incubation among years or colonies should be interpreted taking into account any differences in frequency of temporary abandonment. White-faced Storm Petrels may be able to exploit resources that are farther away from the colony as a result of this egg-neglect (Boersma & Wheelwright, 1979). A recent study by Alho et al. (2022), revealed that White-faced Storm Petrel from Selvagem Grande fed mainly in deep oceanic waters, travelling up to 400 km from the colony, with a tendency for more distant foraging trips during the incubation period (mean of 5.1 days of foraging), as compared with chick rearing period (mean of 3.0 days of foraging). In general, neglecting eggs increases the likelihood of breeding failure in storm petrels (Chaurand & Weimerskirch, 1994; Zangmeister et al., 2009) and can be due to a lack of coordination by mated pairs (Shoji et al., 2011; Zangmeister et al., 2009). For instance, in this population the length of the incubation period varies significantly, with some pairs taking 30% longer than others (Campos & Granadeiro, 1999). Moreover, the risk of predation might be higher as the egg is left alone.

In 2002, mice *Mus musculus* and rabbits *Oryctolagus cuniculus* were eradicated from Selvagem Grande (Oliveira et al., 2010). Even though there has not been a census or breeding monitoring of White-faced Storm Petrels post-eradication, the hatching success in our natural nests is similar to what it was before (Campos & Granadeiro, 1999). Although an alien predator was present at the time, breeding success (53.9% in Campos & Granadeiro 1999) was well within the range of values observed for other petrels

(Warham, 1990) as well as our results of the breeding success of the manipulated natural nests (42% in 2018).

Our data suggests that White-faced Storm Petrel nesting in artificial nests had a better overall breeding performance than birds nesting in natural nests. This pattern seems to have been observed in several seabird species, but factors that increase breeding success inside artificial nests are unclear (e.g., Bried et al., 2009; Bolton et al., 2004; De Leon & Mínguez, 2003; Priddel & Carlile, 1995; Sherley et al., 2012; Wilson, 1986). This suggest that artificial nests may be more secure from predation and from nest structure deterioration, with less risk of disturbance and collapsing than natural sites, especially in long-term monitoring studies. Moreover, digging access entrances to the nest chambers of natural nests may also increase the likelihood of nest depredation (Ambagis, 2004; Huntington et al., 1996).

Breeding success in storm petrels can be affected by intraspecific interactions (Warham, 1990), habitat characteristics (Bolton et al., 2004), predation (Sanz-Aguilar et al., 2009) and/or individual characteristics (e.g., age and breeding experience, Sanz-Aguilar et al., 2009). The diameter and length of the entrance tunnel, which protects the nesting chamber from large predators like gulls, and the size of the nesting chamber, which can only accommodate one breeding pair, would be characteristics selected in the artificial nests (De León & Mínguez, 2003). Additionally, a long-term study by Libois et al. (2012) in the Mediterranean with *Hydrobates pelagicus* showed higher survival rates and breeding success probabilities in artificial nests than in natural nests, possibly as a result of protection from gulls. Yellow-legged gulls *Larus michahellis atlantis* is known to be a predator of White-faced Storm Petrels in our study area (Catry et al., 2010; Matias & Catry, 2010). However, during our fieldwork we did not observe any signs of Yellow-legged gulls' predation on White-faced Storm Petrel, with the exception of one adult found dead outside its artificial nest with signs of predation, possibly from a Yellow-legged gull.

On the other hand, data from the present study and non-systematic observations during fieldwork suggest that Madeiran Wall Lizards might have an impact on White-faced Storm Petrel breeding performance in the manipulated natural nests, although we were unable to test this. Besides the confirmed predated eggs by lizards in the manipulated nests, we also suspect that some of the chick deaths and egg disappearances may be attributed to Madeiran Wall Lizards. Although the disappearance of eggs was the major cause of hatching failure, and we could not determine the cause of these losses, on some occasions during fieldwork, we observed Madeiran Wall Lizards inside nests moving eggs close to the nest entrance. This might not have happened in the artificial nests because the plastic drainage tube could have made it difficult for the egg to be transported to the nest exit. Moreover, no eggs were predated by lizards in the artificial nests. However, only a few hours after hatching, two of the chicks found dead inside the artificial nests were being eaten by lizards. Nonetheless, our study suggests that White-faced Storm Petrels breeding on artificial nests in our study area might achieve a high degree of protection compared to natural nests, mainly until hatching.

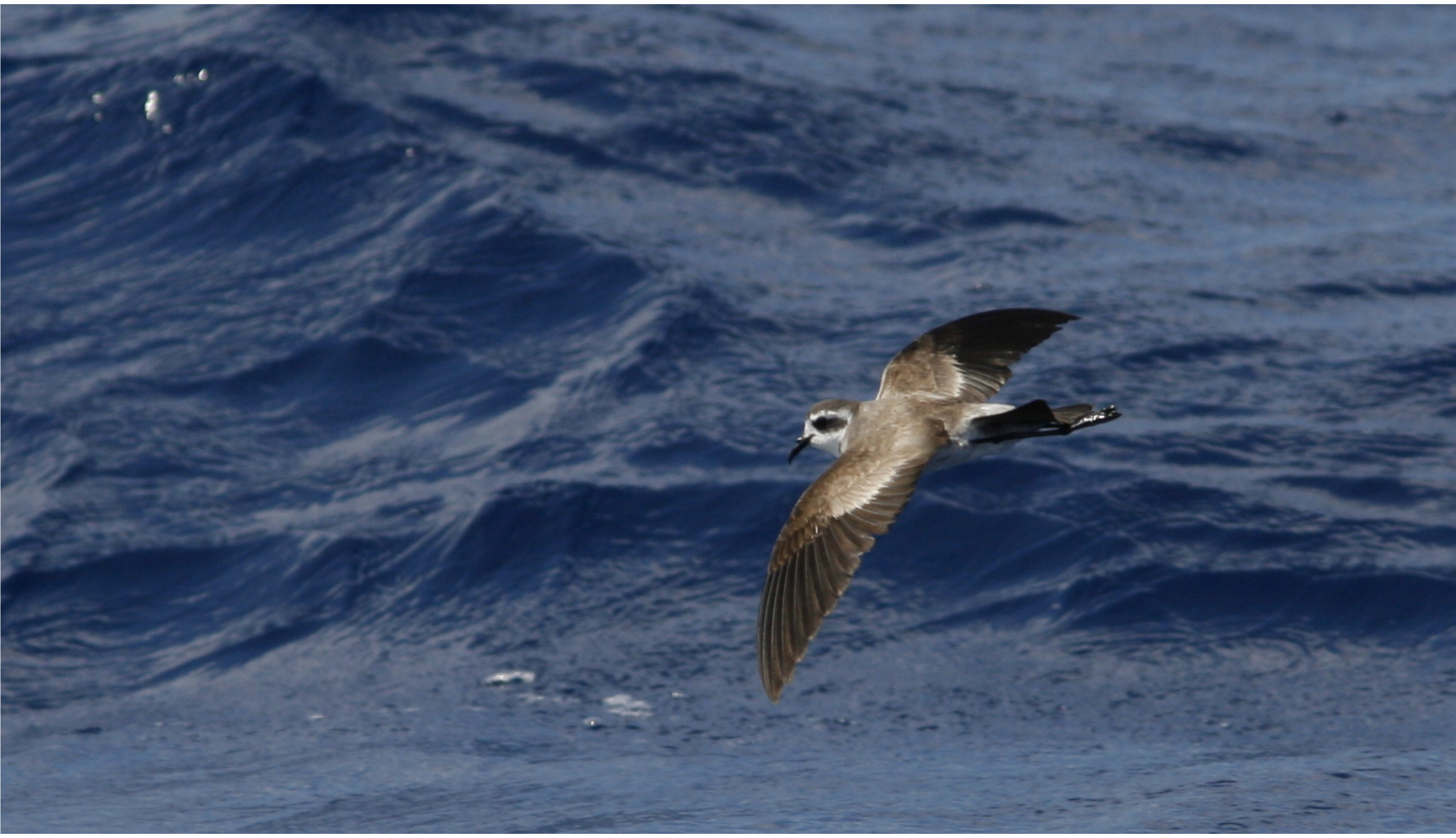
Recent studies by Neves et al. (2017, 2022) also found the first conclusive evidence of the existence of depredation of the endemic Monteiro's Storm petrel chicks by Madeiran Wall Lizards in Azores. They observed lizards dragging a near-fledging chick from its nest. Even though, there is no published post-eradication population study on Madeiran Wall Lizards on the island, it can be inferred that its population may have benefited, given the variety of its diet (Sadek, 1981), its opportunistic behaviour and the absence of native predators. In fact, preliminary data does seem to confirm that the population is increasing (R. Rebelo pers. comm.). Matias et al. (2009) also reported the predation of newly hatched shearwater chicks in Selvagem Grande by Madeiran Wall Lizards. This predation corresponds to a 5% impact on the reproductive success of Cory's shearwater *Calonectris borealis*, and our study suggests that Madeiran Wall Lizards may also have a potential impact over smaller petrel species. In order to understand the effect of lizards on the populations of these smaller species, more research will be required.

Artificial nests must be made of sturdy materials that have a projected lifespan of several years in order to be beneficial over the long-term studies. In this study, artificial nests were built from locally accessible, affordable materials and could easily be produced in large numbers. The longevity of the materials of the artificial nests utilized in the current investigation cannot be determined in the absence of extensive field testing. The artificial nests, since they are buried, do not suffer degradation by sunlight and are also partially protected from temperature variations, but are in permanent contact with the soil and its moist. However, the external lid after two years of use had some signs of degradation. Although it is known that the use of wood and/or plastic in artificial burrows may have an effect on individuals' olfactory capabilities, the current and previous similar studies in other seabird species have shown that adults return to newly installed artificial nests

(Bourgeois et al., 2015; Fromant & Bost, 2020; Gummer et al., 2015). An apparent limitation of our artificial nest design is regarding the diameter of the plastic drainage tube used for White-faced Storm Petrel, as some nests were also occupied by other petrel species (e.g., Bulwer’s petrel), yet the impact seems to be very low from the data presented in our study. We advise the use of a tube with a diameter smaller than 85 mm in any future research with this species, as interference competition for adequate nests can influence hatching success in storm petrels (e.g., Ramos et al., 1997).

Artificial nests have the potential to aid storm petrel conservation, but their use still require careful analysis and a conservative approach. Our study supports the idea that providing artificial nests can help increase nest availability, protect against predation, and possibly encouraging population increases in seabird colonies without disturbance. The installation of artificial nests, along with the observation of natural nests, may prove to be a useful technique for identifying and promoting long-term changes in important demographic parameters.

CHAPTER 6



Ⓒ Killian Mullarney

GENERAL DISCUSSION

The studies in this thesis have contributed to further our understanding of a fascinating and unique group of seabirds: the storm petrels. The work presented in this dissertation encompasses multiple interconnected themes, reviewing the foraging and breeding behaviour of storm petrels (Chapter 2), and provided novel insights into the foraging and breeding behaviour of a distinctive species of storm petrel, the White-faced Storm Petrel *Pelagodroma marina* in a contemporary colony (Chapter 3 and 5). In Chapter 4, we described and characterized an extinct population of this species, while also explored the possible reasons for its extinction. Finally, in Chapter 5, we evaluated the utility of artificial nests as a tool to enhance our knowledge on these small seabirds and potentially aid in conservation efforts. The most relevant conclusions from these studies and directions for future research are summarized below:

In Chapter 2, I undertook the first comprehensive compilation of studies that elucidate the foraging and breeding behaviour of storm petrels, providing a valuable groundwork base for future investigations into these enigmatic seabirds. Nevertheless, for most storm petrel species, numerous fundamental ecological questions remain unanswered, emphasizing the necessity for future research. In addition to their conspicuous size differences, storm petrels possess unique morphological features that lead to distinctive flight patterns and foraging behaviours. These birds are believed to have a heightened sense of smell, which may vary among different species. These variations in olfactory skills or adaptations could play a role in the foraging strategies employed by various species in different contexts.

Storm petrels also rely extensively on public information during the breeding season, which includes cues like the visual, auditory, and olfactory presence of breeding conspecifics, to make decisions about their nesting habitats. Additionally, storm petrels utilize vocalizations in territorial and sexual contexts, with some species' vocalizations receiving more attention from researchers compared to other aspects of their breeding behaviours. This trend is also apparent in published studies examining storm petrel diets, which have seen an increase in recent years, mostly due to a rapid development of more efficient methods, such as high-throughput sequencing techniques (HTS) of DNA barcodes (Valentini et al., 2009).

Understanding how these social cues influence the behaviour of each storm petrel species can be of paramount importance in developing protocols for the restoration of colonies within this group. Storm petrels are notably responsive to recordings of their calls, and successful efforts have been made to establish new colonies using this form of social attraction (Bolton et al., 2004; Podolsky & Kress, 1989)

Despite the long history of observing storm petrels at sea, research on their behaviour and ecology has been relatively slow to develop with a limited number of studies focusing on individual foraging strategies. Only in the past decade that tracking storm petrels has become achievable, regarding the miniaturization of tracking devices. However, notably, the majority of these studies concentrate on Hydrobatidae species, except for the single study on White-faced Storm Petrel in the Northeast Atlantic, which was developed in this PhD thesis (Chapter 3). In Chapter 3, we used 1 g-GPS devices to study the foraging movements of the White-faced Storm Petrel during the incubation and chick rearing periods, focusing on the largest colony of this species in the North Atlantic. The findings indicate that this species exhibited a relatively non-directional departure from Selvagem Grande, primarily utilizing deep oceanic waters, often traveling long total distances of over 700 km during incubation and more than 500 km during chick rearing. While White-faced Storm Petrels did not show a preference for specific population-level foraging hotspots, some individuals did forage near the African coast, the Canary Islands, and along the edge of the continental shelf, especially during chick rearing.

These findings are in line with recent tracking results for other small Procellariiformes species, suggesting that such long-distance foraging is not uncommon among these seabirds. Although, possibly due to their distinct flight behaviour and morphology, White-faced Storm Petrels may have limitations in undertaking exceptionally long foraging trips compared to compared to some Hydrobates species like Leach's Storm Petrel *Hydrobates leucorhous*, known to cover distances up to 1600 km from the colony during the breeding season (e.g., Collins et al., 2022; Halpin et al., 2018; Pollet et al., 2014).

Moreover, the study developed in Chapter 3 also revealed that White-faced Storm Petrel primarily consumed fishes, particularly Myctophidae, and a few cephalopod species, as determined through DNA metabarcoding of chick feaces. The presence of mesopelagic prey in their diet suggests nighttime feeding, when these prey species rise to more superficial waters to feed on zooplankton and also likely driven by underwater predators, which are abundant in the region. This is supported by the marked nocturnal activity recorded in this study, during the chick-rearing phase. Furthermore, mesopelagic prey are commonly found in the diets of other small seabirds nesting in the North Atlantic (Carreiro et al., 2020; Monteiro et al., 1996b, Hedd et al., 2009; Hedd & Montevecchi, 2006; Waap, 2015, Waap et al., 2017; Zonfrillo, 1985).

Surprisingly for us, in our investigation, crustaceans were solely detected in the regurgitated sample from the adult bird and were conspicuously absent from the chick fecal samples. Crustaceans are recognized as important components of the White-faced Storm Petrel diet, as indicated by previous studies (Croxall et al., 1997; Spear et al., 2007; Waap, 2015). This discrepancy in findings can be attributed to several factors. One possible explanation is that the lower DNA yield in fecal samples might have compromised the amplification of crustacean DNA. Another hypothesis suggests that DNA degradation in the feaces could have made crustaceans undetectable by PCR amplification. This might be due to chicks' longer gut retention, efficient assimilation, and digestion, resulting in more degraded DNA. Consequently, fewer identifiable DNA sequences were obtained from chicks compared to adult regurgitates.

Our study also revealed distinct behavioural patterns in White-faced Storm Petrels during incubation compared to chick rearing. Their increased travel speed at night during incubation suggests reduced pattering behaviour and potentially reduced nighttime feeding compared to chick rearing. This shift may be attributed to the higher energy demands of chick rearing, prompting birds to search for prey both day and night, resulting in similar travel speeds throughout the day during this breeding phase. This behaviour also corresponds with their foraging areas, where mesopelagic fish are more abundant in deeper waters rather than shallower continental shelf areas (Gjøsaeter & Kawaguchi; 1980; Nybakken, 2001; Pusch et al., 2004).

Finally, we detected relatively high concentrations of mercury in White-faced Storm Petrels' chick body feathers, supporting the notion that they primarily raise their chicks on mesopelagic prey from deep pelagic areas.

Worldwide, islands have witnessed the tragic disappearance of seabird populations following the arrival of humans and the introduction of invasive species. In Chapter 4 we characterized an extinct seabird colony on Santa Luzia, an uninhabited island in Cabo Verde. Despite no prior reports of seabird extinctions for the island, Santa Luzia yielded a remarkable assemblage of petrel bones within its coastal dunes, and curiously, until our study, these remains remained unidentified. Our investigation encompassed a comprehensive excavation effort and found remains of millions of seabird individuals from five species, including the White-faced Storm Petrel, Boyd's Shearwater, Cabo Verde Storm Petrel, Cabo Verde Shearwater, and *Pterodroma* sp. The radiocarbon dating used in our study indicates that these seabird populations likely went extinct during the first half of the 20th century, possibly due to the arrival of humans and their domestic animals on the island. On Santa Luzia, domestic cats are regarded as a primary threat to native endangered species, strongly suggesting their significant role in the extinction of seabirds on the island. This is further supported by their current predatory impact, which confines Cabo Verde Storm Petrels to inaccessible areas on Santa Luzia (Oliveira et al., 2013). Our data indicates that these seabird populations disappeared relatively swiftly. In contrast, populations on neighboring islands, such as Branco and Raso, endured. This pattern suggests that the extinctions on Santa Luzia resulted from threats localized within the colony, rather than threats at sea, as the latter would likely have impacted neighboring colonies as well. In recent history, Santa Luzia also witnessed the local extinction of the endemic Cabo Verde giant skink *Chioninia coctei*, which was declared extinct in the early 20th century (Mateo, 2012; Schleich, 1996). One factor contributing to its extinction may have included predation by feral cats (Andreone, 2000).

The results presenting in Chapter 4 suggested that Santa Luzia may have been a site of utmost importance as an essential nesting habitat for these species, particularly the White-faced Storm Petrel, given the substantial estimated population size in our study. Notably, we estimated that the population of these extinct seabirds on Santa Luzia was likely in the hundreds of thousands, significantly larger than the current populations of the same species in Cabo Verde (Hazevoet, 2010).

The vulnerability of White-faced Storm Petrel population in Cabo Verde is heightened by the scarcity of nesting habitats free from predators, worsened by soil erosion, which likely limits colony size (Semedo et al., 2020). The small size and few existing colonies make White-faced Storm Petrels highly susceptible to introduced predators and human disturbances, including burrow trampling. Early observations in Cabo Verde indicate that, as with Macaronesia region, smaller seabird species tend to inhabit islets without exotic predators (Oliveira, 2013; Rendall & Pile, 2007; Vasconcelos, 2015), while larger species have a wider distribution, akin to what is seen in the Azores and Madeira (Romano et al., 2010), where medium-sized seabirds like Cory's Shearwater *Calonectris borealis* breed along the cliffs of most islands (Monteiro et al., 1996a).

We suggested further research that focus on enhancing our understanding of potential seabird breeding areas on Santa Luzia and evaluating the seabird colonies on nearby islands as potential sources for future reintroduction efforts. The success of these efforts depends on the complete removal of feral cats from the island, and effective monitoring plans are crucial for any seabird restoration project on Santa Luzia.

As part of our research in Chapter 3, which involved tracking the White-faced storm petrels' foraging behaviour using GPS devices, daily nest monitoring was a crucial component. Careful planning was essential because storm petrels are highly sensitive to nest handling, which can detrimentally affect their nest site fidelity and breeding success (Carey, 2009). To mitigate disturbance risks associated with modifying natural nests, such as burrow collapse and abandonment (Carey, 2009; Warham, 1990; Wilson, 1986), we implemented artificial nests within existing breeding cavities to evaluate their effectiveness in enhancing the breeding performance of White-faced Storm Petrels (Chapter 5). In Chapter 5, we demonstrated that the use of artificial nests is an effective tool for monitoring White-faced Storm Petrels and potentially aiding in their conservation. Our study on Selvagem Grande revealed that the artificial nests, installed within existing breeding burrows, were highly attractive to White-faced Storm Petrels, with notably high occupancy rates (more than 80% in the second breeding season). Moreover, compared to previous studies using artificial nests for storm petrels, our study showed exceptionally high occupancy rates (Bedolla-Guzmán et al., 2016; Bolton, 1996; Bolton et al., 2004; De León & Mínguez, 2003; Libois et al., 2012), possibly attributed to the installation of artificial nests in natural burrows with signs of prior occupation. Temporary egg neglect, as reviewed in Chapter 2 as a common behaviour of storm petrels, was also observed in the artificial nests.

One significant factor contributing to hatching failures in natural nests was egg predation by Madeiran Wall Lizards *Teira dugesii*. Predation on eggs and chicks by Madeiran Wall Lizards was lower in artificial nests than in natural nests, suggesting a higher level of protection in artificial nests, particularly until hatching, although further studies are needed to provide a definitive conclusion. Observations suggested that these lizards might transport eggs within the nests, which may not have occurred in artificial nests due to the design. Moreover, there were no instances of egg predation by lizards in the artificial nests. In conclusion, are artificial nests an important tool for monitoring these small seabirds? Our study demonstrated that they are, especially for long-term monitoring studies, with the added benefit that they could have a potential application in conservation projects.

Future research

Our review on foraging and breeding behaviour of storm petrels has underscored the limited knowledge in this theme and the significance of conducting further research on these unique seabirds. For instance, our understanding of storm petrel movements at sea is still in the beginning, and through this PhD thesis, we present, for the first time, insights into the foraging behaviour of White-faced storm petrels during two breeding seasons in North-east Atlantic. However, this also opens up further questions, such as: Are there differences in foraging strategies between sexes? Are there any differences in diet between chicks and adults? Following the breeding season, where do these seabirds go? Is there a potential segregation of male and female White-faced Storm Petrels in their wintering grounds?

Comprehending the pathways between the breeding and non-breeding grounds is a crucial aspect of the overall ecology of the species and imperative for its conservation. Geolocators may be a useful tool to provide this information. Furthermore, as technology advances, smaller GPS/satellite transmitters could become suitable for studying smaller species. The prospect of utilizing space-based systems could also hold value in tracking the movements of these small seabirds. Continued tracking studies on storm petrels and at various colonies will yield crucial insights into the variability of marine movements and habitat utilization among different years, locations, and species. This data will also aid in identifying the specific threats that various populations may encounter at sea. Moreover, combining remotely-sensed oceanographic data with data on diet and on movements will investigate the influence of spatial and temporal variability on the availability of different prey types.

Enhancing our comprehension of storm petrels' foraging behaviour necessitates investigations into their dietary habits. This would enable us to correlate marine habitat selection with food availability and forecast potential impacts of environmental changes on prey species and habitat utilization. Furthermore, a more comprehensive understanding of population dynamics, demographic rates, marine movements, and diet would establish essential foundational data for a holistic assessment of the influence of human activities on these species.

Being situated as lower trophic level consumers, such as zooplankton feeders, storm petrels possess the capability to detect environmental shifts at an accelerated rate when compared to larger seabirds (Grémillet et al., 2015). In our study, White-faced Storm Petrel chicks exhibited relatively high mercury concentrations in their feathers, although there is currently insufficient data to evaluate cumulative mercury effects on seabird populations. Nonetheless, smaller seabird species like White-faced Storm Petrels can serve as bioindicators of marine conditions and sentinel species for environmental changes.

Our study vividly demonstrates the substantial impact of an invasive predator on a seabird colony, highlighting how swiftly it can drive a species, especially smaller seabirds like storm petrels, toward extinction. Determining effective conservation strategies for storm petrels is challenging due to limited knowledge of their ecology and behaviour. Eradicating invasive species on suitable island habitats can lead to the rapid recolonization of storm petrels and long-term monitoring of demographic factors including survival and breeding success is crucial for understanding population changes and guiding conservation efforts. Installing and maintaining artificial nests at key breeding sites can facilitate this monitoring, especially since many natural nest sites are inaccessible, as we demonstrated in our research. Provision of artificial nests is also a valuable tool for closely monitoring demographic changes in seabird populations. While potential differences between natural and artificial nests should be considered, our study shows that White-faced Storm Petrels nesting in artificial nests had a better overall breeding performance than birds nesting in natural nests. Our study also highlighted the possible impact of predators like lizards on other petrel species and emphasized the need for further research to assess their effects on smaller petrel species.

The rehabilitation of disturbed islands is crucial to protect ecologically critical storm petrel populations. Furthermore, long-term studies, such as those provided by paleoecological approaches, are required to better understand shifting baselines in conservation to truly recognize current rates of ecological loss. Despite the challenges in studying storm petrels, this research has provided new insights into White-faced Storm Petrel behaviour and ecology in the North-east Atlantic. It has also highlighted critical knowledge gaps that need addressing for the study and conservation of storm petrels.

Crucially, future research endeavors should prioritize gaining insight into the fundamental ecology of most storm petrel species, given the limited knowledge about their behaviour within colonies and at sea. As we address the knowledge gaps highlighted here, our comprehension of foraging and breeding behaviours in storm petrels will continue to develop.

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APPENDIX A

GLOBAL ASSESSMENT OF MARINE PLASTIC EXPOSURE RISK OF OCEANIC BIRDS

Clark, B. L., Carneiro, A. P. B., Pearmain, E. J., Rouyer, M. M., Clay, T. A., Cowger, W., Phillips, R. A., Manica, A., Hazin, C., Eriksen, M., González-Solís, J., Adams, J., Albores-Barajas, Y. V., Alfaro-Shigueto, J., Alho, M. S., Araujo, D. T., Arcos, J. M., Arnould, J. P. Y., Barbosa, N. J. P., Barbraud, C., Beard, A. M., Beck, J., Bell, E. A., Bennet, D. G., Berlincourt, M., Biscoito, M., Bjørnstad, O. K., Bolton, M., Booth Jones, K. A., Borg, J. J., Bourgeois, K., Bretagnolle, V., Bried, J., Briskie, J. V., Brooke, M. L., Brownlie, K. C., Bugoni, L., Calabrese, L., Campioni, L., Carey, M. J., Carle, R. D., Carlile, N., Carreiro, A. R., Catry, P., Catry, T., Cecere, J. G., Ceia, F. R., Cherel, Y., Choi, C. Y., Cianchetti-Benedetti, M., Clarke, R. H., Cleeland, J. B., Colodro, V., Congdon, B. C., Danielsen, J., De Pascalis, F., Deakin, Z., Dehnhard, N., Dell'Omo, G., Delord, K., Descamps, S., Dilley, B. J., Dinis, H. A., Dubos, J., Dunphy, B. J., Emmerson, L. M., Fagundes, A. I., Fayet, A. L., Felis, J. J., Fischer, J. H., Freeman, A. N. D., Fromant, A., Gaibani, G., García, D., Gjerdrum, C., Gomes, I. S. G. C., Forero, M. G., Granadeiro, J. P., Grecian, W. J., Grémillet, D., Guilford, T., Hallgrimsson, G. T., Halpin, L. R., Hansen, E. S., Hedd, A., Helberg, M., Helgason, H. H., Henry, L. M., Hereward, H. F. R., Hernandez-Montero, M., Hindell, M. A., Hodum, P. J., Imperio, S., Jaeger, A., Jessopp, M., Jodice, P. G. R., Jones, C. G., Jones, C. W., Jónsson, J. E., Kane, A., Kapelj, S., Kim, Y., Kirk, H., Kolbeinsson, Y., Kraemer, P. L., Krüger, L., Lago, P., Landers, T. J., Lavers, J. L., Le Corre, M., Leal, A., Louzao, M., Madeiros, J., Magalhães, M., Mallory, M. L., Masello, J. F., Massa, B., Matsumoto, S., McDuie, F., McFarlane Tranquilla, L., Medrano, F., Metzger, B. J., Militão, T., Montevecchi, W. A., Montone, R. C., Navarro-Herrero, L., Neves, V. C., Nicholls, D. G., Nicoll, M. A. C., Norris, K., Oppel, S., Oro, D., Owen, E., Padget, O., Paiva, V. H., Pala, D., Pereira, J. M., Péron, C., Petry, M. V., de Pina, A., Pina, A. T. M., Pinet, P., Pistorius, P. A., Pollet, I. L., Porter, B. J., Poupart, T. A., Powell, C. D. L., Proaño, C. B., Pujol-Casado, J., Quillfeldt, P., Quinn, J. L., Raine, A. F., Raine, H., Ramírez, I., Ramos, J. A., Ramos, R., Ravache, A., Rayner, M. J., Reid, T. A., Robertson, G. J., Rocamora, G. J., Rollinson, D.

P., Ronconi, R. A., Rotger, A., Rubolini, D., Ruhomaun, K., Ruiz, A., Russell, J. C., Ryan, P. G., Saldanha, S., Sanz-Aguilar, A., Sardà-Serra, M., Satgé, Y. G., Sato, K., Schäfer, W. C., Schoombie, S., Shaffer, S. A., Shah, N., Shoji, A., Shutler, D., Sigurðsson, I. A., Silva, M. C., Small, A. E., Soldatini, C., Strøm, H., Surman, C. A., Takahashi, A., Tatayah, V. R. V., Taylor, G. A., Thomas, R. J., Thompson, D. R., Thompson, P. M., Thórarinsson, T. L., Vicente-Sastre, D., Vidal, E., Wakefield, E. D., Waugh, S. M., Weimerskirch, H., Wittmer, H. U., Yamamoto, T., Yoda, K., Zavalaga, C. B., Zino, F. J., & Dias, M. P.

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A1. ABSTRACT

Plastic pollution is distributed patchily around the world's oceans. Likewise, marine organisms that are vulnerable to plastic ingestion or entanglement have uneven distributions. Understanding where wildlife encounters plastic is crucial for targeting research and mitigation. Oceanic seabirds, particularly petrels, frequently ingest plastic, are highly threatened, and cover vast distances during foraging and migration. However, the spatial overlap betweenpetrels and plastics is poorly understood. Here we combine marine plastic density estimates with individual movement data for 7137 birds of 77 petrel species to estimate relative exposure risk. We identify high exposure risk areas in the Mediterranean and Black seas, and the northeast Pacific, northwest Pacific, South Atlantic and southwest Indian oceans. Plastic exposure risk varies greatly among species and populations, and between breeding and non- breeding seasons. Exposure risk is disproportionately high for Threatened species. Outside the Mediterranean and Black seas, exposure risk is highest in the high seas and Exclusive Economic Zones (EEZs) of the USA, Japan, and theUK. Birds generally had higher plastic exposure risk outside the EEZ of the country where they breed. We identify conservation and research priorities,and highlight that international collaboration is key to addressing the impactsof marine plastic on wide-ranging species.

A2. INTRODUCTION

Plastic pollution harms marine life worldwide[1], alongside other threats including fishing, climate change and invasive species[2]. Reports of entanglement and ingestion impacts are mounting[1,3,4], but there are large gaps in our understanding, including about factors affecting plastic encounter, ingestion rates, mortality and population-level impacts[4,5]. Marine plastic is unevenly distributed[6], accumulating in patches within ocean gyres and coastal regions[7,8], and often drifting thousands of kilometres in ocean currents[8,9]. Likewise, marine life is patchily distributed[10], and many species cross oceans and political boundaries[11,12]. With plastic production and waste generation continuing to increase[13], identifying at-risk species and populations is crucial for targeting conservation action and research[14–16] because the vulnerability of populations relates to exposure to a hazard, sensitivity to damage that impacts survival or reproduction, and the resilience of the population[17].

Many seabird species are sensitive to plastic pollution; they frequently ingest plastic[1], which can have lethal and sublethal impacts caused by chemical contamination[18] and physical damage or blockages[19]. Numerous factors affect the amount of plastic accumulated by different species including foraging behaviour, at-sea distribution and gut morphology[20–22]. Among seabirds, albatrosses and petrels can contain particularly high loads of plastic ingested directly or within their prey[1,20]. Many species rarely regurgitate indigestible items, except when feeding their chicks[23]. Petrels are particularly sensitive because they retain plastic for long periods due to their gut morphology[22], and small species (e.g., storm-petrels and gad*fl*y petrels) can suffer greater physical damage or higher metabolic costs from ingesting plastic relative to larger species[5]. Petrels are a diverse group of 123 wide-ranging species that inhabit all the world's oceans, making them good sentinels for ocean health[2]. Many populations are unlikely to be resilient to hazards because over half (64) are listed as globally Threatened or Near Threatened by the International Union for the Conservation of Nature (IUCN), including 16 Endangered and 12 Critically Endangered species[2]. Moreover, we know little about the status of many of their populations or if they are impacted by plastic[2].

Assessing risk to petrel populations from plastic pollution requires a robust understanding of vulnerability to ingestion, for which exposure at sea is a key component[14]. Seabirds risk encountering plastic when they forage near sources associated with dense human populations[24], fisheries[25] and shipping lanes[26], or in mid-ocean gyres where floating debris accumulates[27–29]. Exposure risk can be characterised by estimating contact between organisms and hazards, or their co-occurrence, and a key goal in ecological risk assessment is to consider variation in the amount of time spent by animals in different parts of their range[30,31]. Plastic exposure risk has not been previously quantified using methods that account for the time spent in areas of different densities of plastic pollution, but lightweight tracking devices have recently provided unprecedented detail about the movements of petrels of all sizes[32], including the time spent in different foraging areas and across the annual cycle[33].

Here, we estimate relative marine plastic exposure risk for 77 petrel species at a global scale by calculating the spatiotemporal overlap between modelled floating plastic density and the space-use of tracked birds[14]. To inform conservation action and future research, we compare exposure risk across populations, seasons (breeding and non-breeding), Exclusive Economic Zones (EEZ) and areas beyond national jurisdiction (the high seas), and found substantial variation. We identified areas of high risk of exposure to plastic debris in the Mediterranean and Black seas, the northeast Pacific, the northwest Pacific, the South Atlantic and the southwest Indian Ocean. Our results also reveal that Threatened species have greater exposure risk. Because marine debris and seabirds cross multiple political boundaries, our results emphasise that efforts to reduce the amount of plastic waste in the ocean should not only focus on areas of high exposure risk. Improved international cooperation and collaboration are needed to address this global threat.

A3. RESULTS AND DISCUSSION

A3.1. PLASTIC EXPOSURE RISK FOR PETRELS

We analysed 1,736,880 tracked locations for 7137 adults of 77 petrel species (64% of species within Oceanitidae, Hydrobatidae and Procellariidae, excluding the two *Macronectes* species), from 148 populations in 27 countries and Antarctica, between 1995 and 2020 (mean = 2012). For each population, we calculated monthly 95% utilisation distributions (UDs) that estimate time spent by tracked petrels in 10 km grid cells (i.e., smoothed density of 12-hourly tracked locations; Fig. 1a), and combined monthly UDs into seasons (breeding or non-breeding). If data were available from multiple populations of a species, we created species UDs weighted by approximate population size. We calculated a geometric mean of global marine plastic densities estimated by three published models[6,9,34] for micro- and macro-plastics (~0.333 mm–40 cm) combined for 2014 in 1 × 1° cells (Fig. 1b). We aggregated petrel UDs into 1 × 1° grid cells and created an all-species map by summing species UDs, weighting those tracked only in the breeding season and so not including the non-breeding part of the annual cycle at 0.5 (Fig. 1c). We divided the plastic and petrel grids by their respective cumulative sums so that the values of each global grid summed to one. We then multiplied each petrel UD by the plastic density to map spatial overlap as an indicator of estimated exposure risk[14] (e.g., Figure 1d). Summing the values across cells provided an exposure risk score, which we multiplied by 10^6 to provide an easy-to-use scale; this gave us monthly population-level scores ranging from 0.0007 to 1091.

We ranked species by plastic exposure risk score (Fig. 2a), ranging from 0.003 to 549 (mean = 28.0; median = 4.9, interquartile range = 1.8–14.5). Of particular concern are the 19 species scoring over 15.3 (the score any species would receive if plastic was evenly distributed worldwide), indicating they mostly use areas with above-average plastic density. These species include the Critically Endangered Balearic shearwater *Puffinus mauretanicus* and Newell's shearwater *Puffinus newelli*; the Endangered Hawaiian petrel *Pterodroma sandwichensis*; and the Vulnerable yelkouan shearwater *Puffinus yelkouan*, Cook's petrel *Pterodroma cookii* and spectacled petrel *Procellaria conspicillata* (Fig. 2a). The proportion of total exposure risk within each IUCN Red List category differs from the proportion of tracked species within each category, with a greater percentage of the exposure risk shared among Threatened species, particularly Critically Endangered species (Fig. 2b). The 20 highest-scoring species had greatest plastic exposure risk in five areas, both in coastal regions (Mediterranean/Black Sea, northwest Pacific) and ocean gyres (north-east and northwest Pacific, South Atlantic, southwest Indian oceans; Figs. 1d, 2a). Plastic exposure risk was low in upwelling zones (Humboldt and Canary currents) and polar regions (Fig. 1d). For some species, scores differed greatly among populations (Fig. 2a). For example, European storm-petrels *Hydrobates pelagicus* breeding in the Mediterranean had much higher scores (306–534) than elsewhere (1.0–1.4;

Supplementary Fig. 1). There was no long-term trend in exposure risk scores for populations tracked in the same months for more than three years (Supplementary Fig. 2). By using tracking data to estimate the relative density of regularised bird locations, instead of using only estimated presence or absence, we explicitly consider spatio-temporal variation in seabird distributions, thus providing more detail on global plastic exposure risk for a subset of species than an analysis based on range maps, which inferred different geographic hotspots of plastic exposure risk[14].

A3.2. BREEDING AND NON-BREEDING SEASON EXPOSURE RISK

We calculated breeding and non-breeding plastic exposure risk scores for 107 populations of 60 species. The mean difference between sea-sons was 34.0, with little difference for most populations (median = 3.6), but substantial differences for some (maximum = 521.8; Fig. 3a). For example, Scopoli's shearwaters *Calonectris diomedea* breed on Malta in the Mediterranean and migrate to the eastern Atlantic Ocean where they had a much lower plastic exposure risk score (30.0) than during the breeding season (496.2). In contrast, yelkouan shearwaters also breed on Malta (517.5), but had a higher score during non- breeding (937.7) when they disperse within the Mediterranean and migrate to the Black Sea (Fig. 3a–c). Seasonal contrasts also varied among populations of the same species. For example, scores for Cook's petrels during non-breeding were much higher for birds breeding in northern New Zealand that migrate to the northeast Pacific (159.3), than those breeding in southern New Zealand that migrate to the Humboldt Current (0.8; Fig. 3a, d, e).

A3.2. EXPOSURE RISK AND INGESTION

Plastic exposure risk, as indicated by our scores, is necessary but not sufficient for ingestion to occur and there are not yet enough suitable samples to quantify this process for most species. The amount of ingested plastic detected in seabirds is affected by foraging style, body size, tendency to regurgitate, gut morphology, prey type, age and breeding stage[20,22,23,28]. Few ingestion studies have used standardised protocols to sample different populations of the same species[4]. Furthermore, ingestion data are influenced by whether samples came from pellets[26] or regurgitates[18], or necropsies of birds that were found dead at a colony[29] or on beaches[35], recovered after attraction to light pollution[36], bycaught in fisheries[37], or taken for research[28] or human consumption[4]. Nonetheless, studies that compared ingestion for different populations of the same species using the same methods control for these factors, and so can be compared to our exposure risk scores. For example, flesh-footed shearwaters *Ardenna carneipes* sampled in eastern parts of their breeding range contained significantly more plastic[20], consistent with our higher scores during the non-breeding season for populations migrating to the northwest Pacific (New Zealand = 44.9; Lord Howe = 47.1) compared with those migrating to the eastern Indian Ocean (Western Australia = 13.6). Additionally, the Ecological Quality Objective for part of the North Sea target of <10% of northern fulmars *Fulmarus glacialis* containing ≥0.1 g of plastic was exceeded more in the North Sea than Arctic Canada[38], mirroring our exposure risk scores for those tracked from the UK (1.4) and Canada (0.25). There are clear examples of high ingested plastic loads in high exposure risk areas in the Mediterranean[37], northeast Pacific[39] and southwest Indian Ocean[36]. However, plastic loads are both low and high in areas with low exposure risk[40], indicating that birds may still be at risk while foraging in marine areas with low estimated plastic densities. Plastic has been ingested even by the species with the lowest exposure risk score of 0.003 (4% of 27 sampled snow petrels *Pagodroma nivea*, which forage around Antarctica, contained plastic[40]), indicating that the ubiquitous availability of plastic is concerning across all oceans worldwide, not only in areas where plastic aggregates.

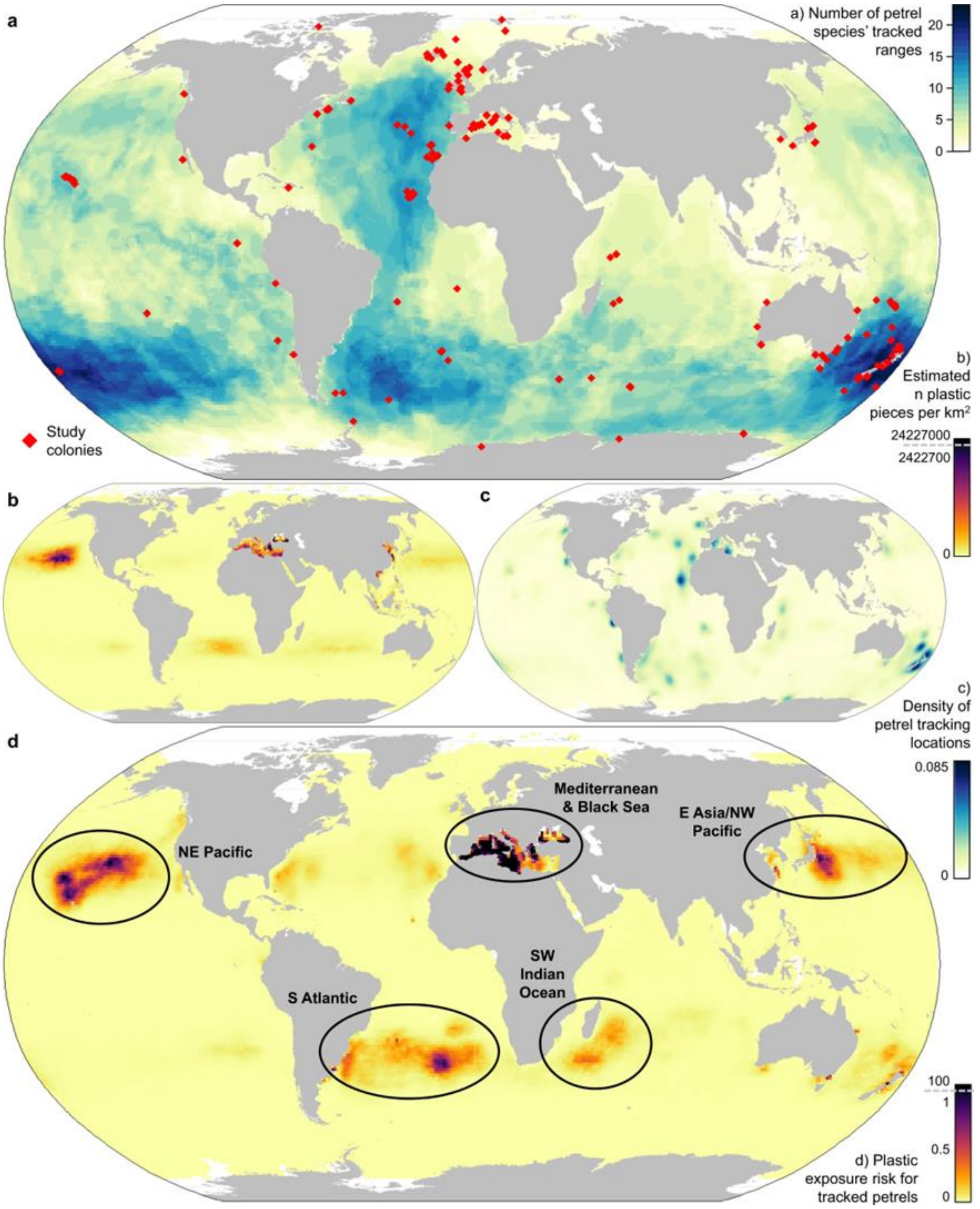

Fig. 1 Mapping petrels and plastics. **a** Species richness based on presence within 95% utilisation distributions isopleth contours from tracking data for 77 petrel species. Red diamonds indicate the colonies from which tracking data were obtained. **b** Plastic density at the ocean surface, showing the square root of the number of plastic pieces (~0.333 mm–0.4 m) estimated per km^2 in each 1 × 1° grid cell. For visualisation only, the values are capped at 10% due to extreme values. **c** Summed 95% utilisation distributions for all species, with species weighted equally if year-round tracks were available or by 0.5 if tracks were only available forthe breeding season. If we had data from multiple populations for a species,

densities were weighted by approximate population size. **d** Exposure risk to plastic was calculated by multiplying the density value in each cell for plastics (scaled to sum to 1) by the value for petrels (scaled to sum to 1). For visualisation only, the values are capped at 1% due to extreme values, and all other values are shown on a linear scale. Black ellipses relate to the areas identified from the 20 species with the highest exposure risk scores (Fig. 2a). *n* = number. White = no data. Robinson Projection. Land polygons from Natural Earth. Source data for colony locations are provided as a Source Data file

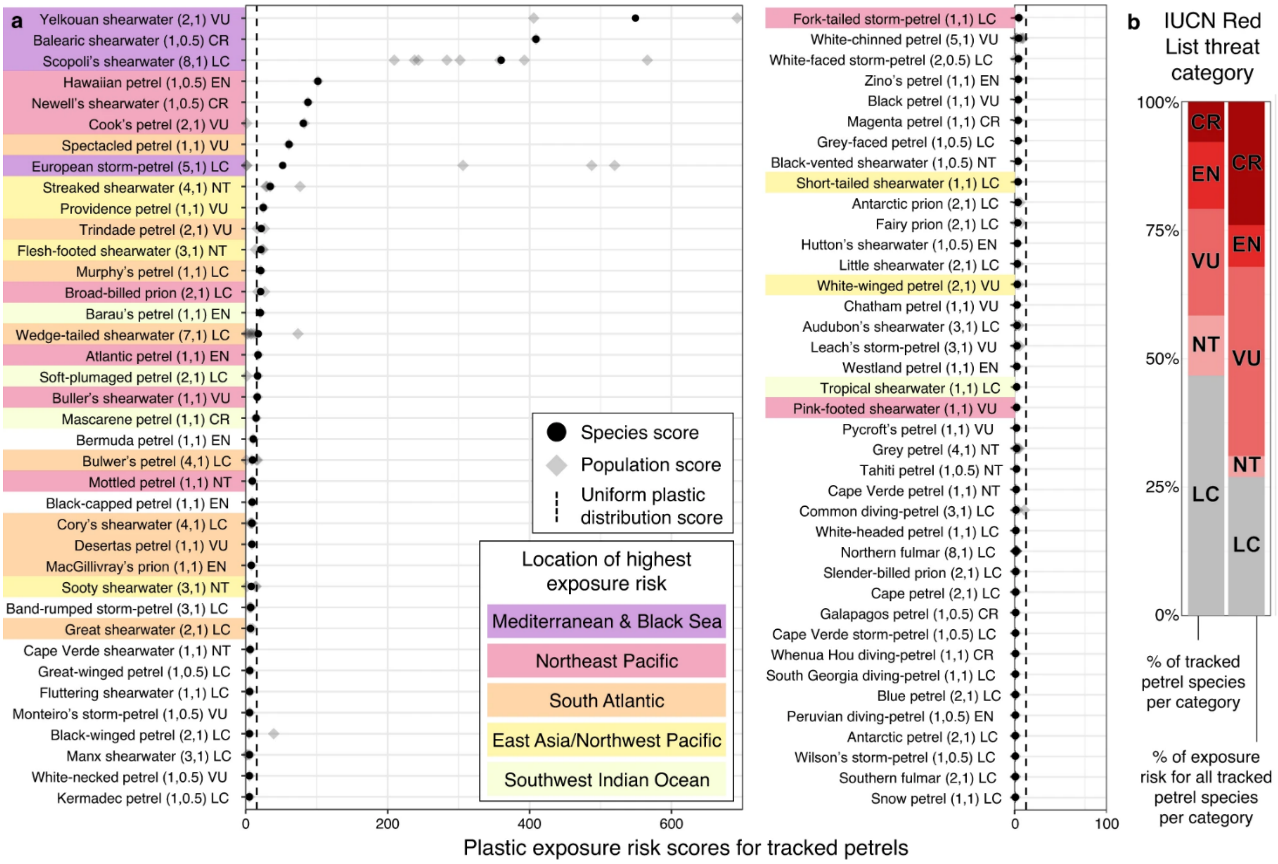

Fig. 2 Plastic exposure risk scores for 77 petrel species. **a** Species are ranked by exposure risk from the top-left to the bottom-right. Colours represent the location that contributed most to the score for the five areas of highest exposure risk. Where there are multiple populations per species (grey diamonds), the mean of all populations (black circles) is weighted by the population size. The vertical dashed line indicates the theoretical exposure risk score if plastic was uniformly distributed across all cells (15.3). Values in parentheses are the number of populations, followed by 1 if the species was tracked in breeding and non-breeding seasons or by 0.5 if only tracked in one season. Two-letter codes indicate the IUCN Red List assessment threat category (Least Concern (LC; *n* = 36), Near Threatened (NT; 9), Vulnerable (VU; 16), Endangered (EN; 10), Critically Endangered (CR; 6)). **b** The percentage of tracked petrel species within each IUCN threat category and the percentage of total exposure risk attributed to species in each category. Source data are provided as a Source Data file.

A3.4. JURISDICTIONS AND POLICY

Plastic exposure risk for tracked petrels occurred mostly in the Mediterranean and Black Seas (Fig. 4a, b), where breeding European storm- petrels and Scopoli's, yelkouan and Balearic shearwaters are at risk, with high plastic loads recorded[37,41]. Elsewhere, the high seas are used by 75 of our 77 tracked species, and accounted for 25% of global plastics exposure risk, mainly within oceanic gyres. The US EEZ accounted for a high proportion of the exposure risk, noticeably northeast of Hawai'i, followed by the EEZs of Japan, and the UK, mainly around the Overseas Territories of Tristan da Cunha and Bermuda (Fig. 4a, b). The New Zealand EEZ ranked highly despite low plastic levels due to the exceptionally high petrel occurrence and diversity. Moderate plastic exposure risk scores (0.15–1.00% of total) occurred in the EEZs of France, Australia, Brazil, Portugal, Mauritius, China, Russia, Argentina, Madagascar, Bahamas, and Mexico (Fig. 4a).

Our results indicate that mitigating plastic pollution in the breeding country's EEZ alone would not adequately protect most species throughout the annual cycle. We identified links between the countries within which each tracked petrel population breeds (including overseas territories) and the jurisdictions where those populations were exposed to plastic (Fig. 4c). Exposure risk primarily occurred outside the breeding country's EEZ (theoretical EEZ in the Mediterranean because actual EEZs are not clearly defined), except for 7 of the 29 highest-scoring populations (e.g., wedge-tailed shearwaters *Ardenna pacifica* in the USA, and streaked shearwaters *Calonectris leucomelas* in Japan). Of the 29 highest-scoring populations, 25 were exposed to plastic in multiple EEZs. For example, streaked shearwaters breeding in South Korea were exposed in China, Malaysia, the Philippines, South Korea, Indonesia and Vietnam (Fig. 4c). Exposure risk was greatest in the high seas for 15 of the 29 highest-scoring populations, particularly those breeding in the USA, New Zealand, UK, Brazil, Australia, France, and Mauritius (Fig. 4b). For each petrel population, we provide the percentage of exposure risk occurring in each EEZ and the high seas to facilitate targeting mitigation and policy efforts towards key areas (Supplementary Data 1).

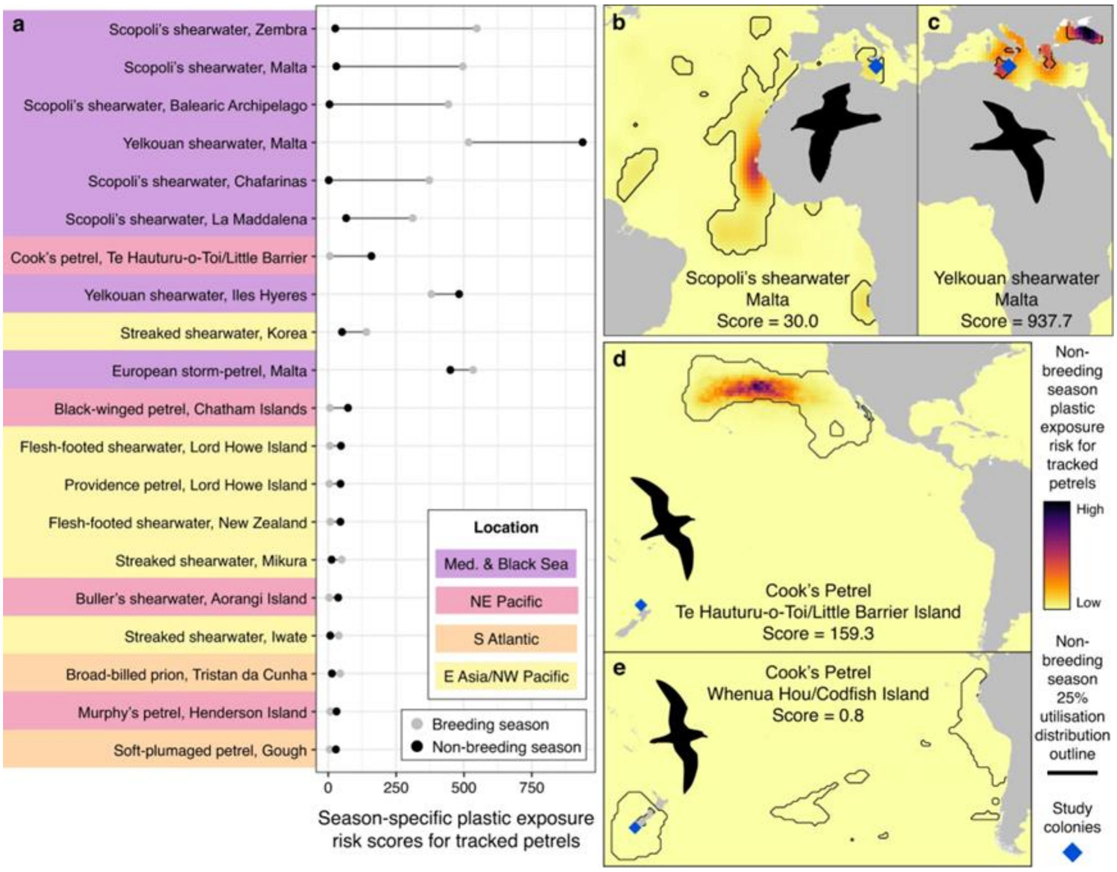

Fig. 3 Sason-specific plastic exposure risk scores. **a** Scores during breeding (grey circles) and non-breeding seasons (black circles) for the 20 populations with the greatest differences between seasons (grey lines). **b** Non-breeding season plastic exposure risk for Scopoli's shearwaters (non-breeding score = 30.0, breed- ing season score = 496.24) and **c** yelkouan shearwaters (non-breeding = 937.7, breeding =517.5) for tracked from Malta, and for Cook's petrels breeding either at **d** Te Hauturu-o-Toi/Little Barrier Island (non-breeding = 159.3, breeding = 5.5) or **e** Whenua Hou/Codfish Island (non-breeding = 0.8, breeding = 2.1). Black lines indicate the outline of the most used area in the non-breeding season (top 25% ofthe utilisation distribution). Land polygons from Natural Earth. Source data are provided as a Source Datafile.

Marine vertebrates and plastic debris are globally distributed andhighly mobile, and cross political boundaries within and beyond national jurisdictions[11]. Therefore, mitigating plastic pollution frommarine and terrestrial sources will require efforts targeted across multiple jurisdictions and the high seas[42]. International cooperation, collaboration, resource mobilisation and information exchange are key to addressing marine plastic pollution[43] by limiting still-increasing plastic waste production[13], improving waste management, and cleaning up existing plastic. The International Convention for the Prevention of Pollution from Ships (MARPOL) Annex V prohibiting plastic waste discharge from vessels entered into force 31st December 1988[44], but plastics from marine sources still affect seabirds[26] and account for at least 22% of ocean plastics[45]. Ghost fishing gear is a priority because it presents deadly entanglement risk[25] and food web contamination after degradation at sea. Pollution from vessels could be reduced with more resources and incentives for monitoring and managing waste, and enforcing MARPOL and local regulations, particularly among developing countries[46]. A coordinated approach for plastic waste management could be achieved, for instance, through a global-scale treaty on plastics[43], which could operate in synergy with MARPOL and other relevant bodies and frameworks, such as the Convention on Biological Diversity, Convention on the Conservation of Migratory Species, Agreement on the Conservation of Albatrosses and Petrels, Regional Seas Conventions and Action Plans.

A3.5. RESEARCH PRIORITIES

Greater use of standard methods for future ingestion studies would facilitate comparison and help identify the drivers of plastic ingestion[4,47]. The relationship between exposure risk, ingestion and impact could be examined by concurrently sampling ingested plastic and tracking movements[41,48], and measuring physiological impacts. Interspecific differences could be clarified by systematically comparing plastic loads in species that have similar geographic ranges and exposure risk scores. Crucially, it is unclear for which species or populations plastic ingestion reduces survival or productivity and how much exposure they can tolerate; so, studies of population-level impacts and how to separate these from known causes of population declines will be vital[2,5]. Four species with high plastic exposure risk scores but no ingestion data in a recent review[1] are key research priorities: Hawaiian petrel and streaked shearwater within the main high-exposure risk areas, and Bermuda petrel *Pterodroma cahow* and Desertas petrel *Pterodroma deserta* elsewhere. Comparable ingestion data from different tracked populations of the same species with contrasting migration patterns (e.g., Cook’s petrel; Fig. 3d, e) would be particularly valuable.

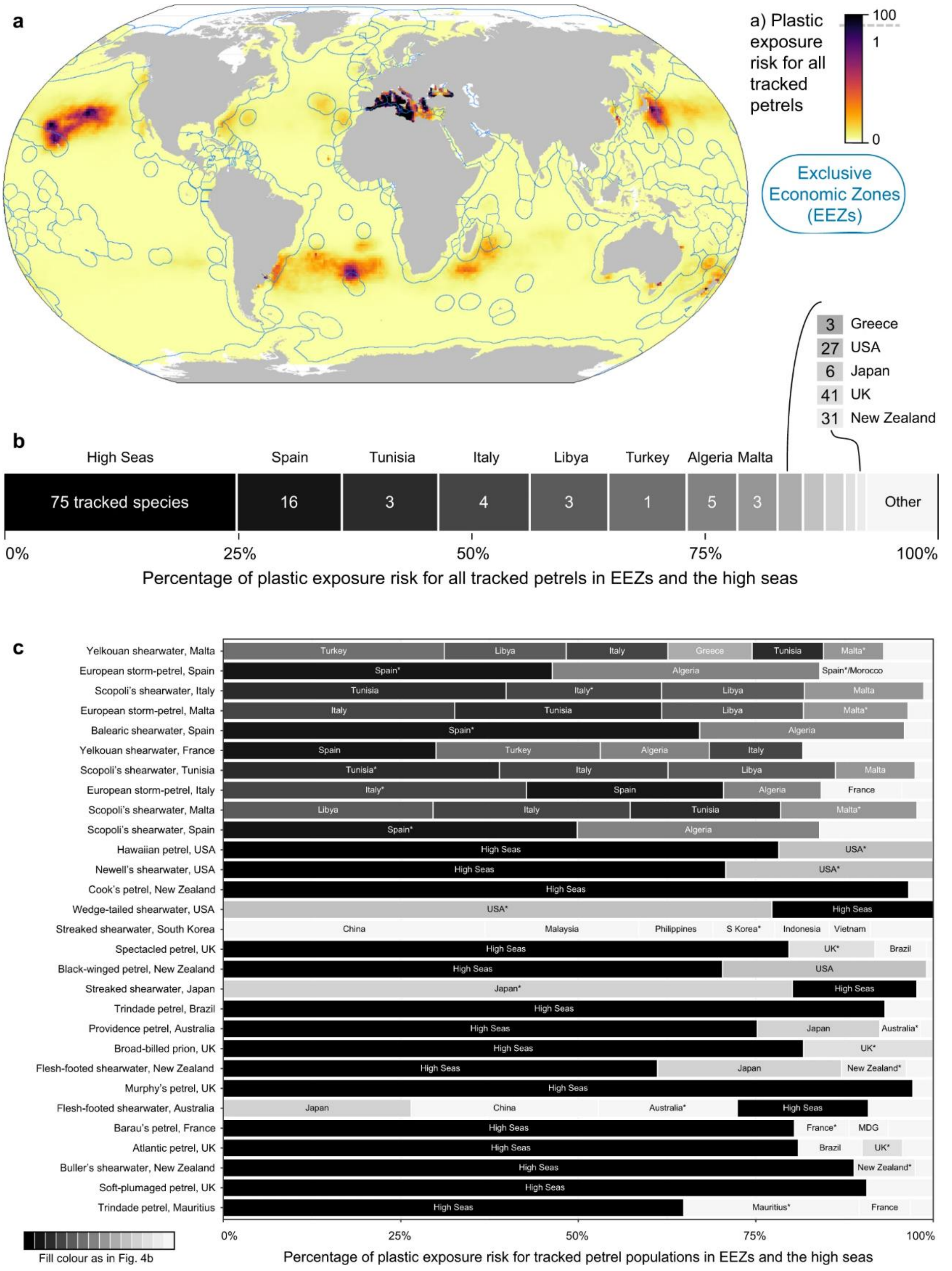

Fig. 4 Plastic exposure risk for petrels in different jurisdictions. **a** Map of plastic exposure risk for 77 petrel species in the Exclusive Economic Zones (EEZs) ofeach country (including overseas territories) and the high seas (Areas Beyond National Jurisdiction). In the Mediterranean, theoretical EEZs are used. For visua-lisation only, the score is capped at 1% due to extreme values in the Mediterraneanand Black Seas. **b** The percentage of plastic exposure risk score attributed to thehigh seas and each EEZ/theoretical EEZ

accounting for >1% of total exposure risk, labelled with the number of tracked species using each area (values are provided in Supplementary Table 1). **c** For the 29 petrel populations by country with the highest exposure risk scores (ranked from high to low), bars show the proportion of the exposure risk score in each jurisdiction that accounts for over 5% of the total exposure risk, with unlabelled bars containing all others. Bars are coloured according to **b**. Overlapping territorial claims are shown as claim 1/claim 2. MDG = Madagascar. Asterisks(*) indicate that the EEZ matches the breeding country. Land polygons from Natural Earth. Source data are provided as a Source Data file

Our tracking data covered almost all of the world's oceans and all ocean regions within the ranges of 70% of analysed species, broadly matching seabird biodiversity in general[10], but also reflecting known spatial biases in research effort, notably towards the Atlantic Ocean and latitudes south of 40°S[32] (see Supplementary Table 2 for spatial coverage gaps). Our study included tracking data for all four petrel species that breed in the Mediterranean, but we identified 14 species that occur in other high-exposure risk areas, making them priorities for tracking studies (Supplementary Table 3). Additionally, both petrel tracking and ingestion data are sparse in coastal waters around east and southeast Asia, where high plastic densities occur, and the South Pacific and North Atlantic gyres, where moderate plastic densities occur[10,32] (Fig. 1). We identified priority species for future research in each of these regions (Supplementary Table 4). Sample sizes varied substantially among species, from 3 to 960 individuals (median = 35, mean = 93), so additional tracking for some species could be beneficial (Supplementary Data 2). Furthermore, tracking immature birds or adults when deferring breeding could reveal differences in exposure risk[33]. Our method could also be applied to global-scale, multi-species tracking datasets[12] for other marine megafauna, such as turtles and marine mammals, for which plastic pollution is also a threat[1].

Collecting more data on plastic density, identifying sources, and developing density models to provide better spatial coverage at a higher resolution would aid targeted mitigation strategies, and enable a better understanding of the effects of spatial scale on plastic expo-sure risk. The models that produced the plastic density estimates used in our analysis involved interpolating over wide areas, whereas observed plastic densities tend to be more patchy[49]. There were limited plastic data, particularly for southeast Asia[6], where a recent survey recorded high plastic levels[50]. The South Pacific has a high petrel species richness, but few samples were used to inform the plastic density models[6]. The plastic density model estimates covered most of the Arctic and Antarctic oceans, but had more missing values near the poles than in other regions (Fig. 1b), although the Southern Ocean is not thought to contain much plastic[6]. However, plastic accumulates around Svalbard in the Arctic[51], which although only important for northern fulmars among petrels, could affect other taxa. Marine species also feed at different depths and so it would be valuable to examine how plastic varies vertically[52]. Repeated plastic sampling across longer timescales would improve temporal matching between plastic and seabird data and allow investigations into long-term changes in plastic exposure risk[53]. We provide example versions of the code used to produce our results to facilitate future research on different tracking or plastics datasets[54].

A4. METHODS

In brief, we collated tracking data for petrels and computed gridded utilisation distributions (UDs) at a monthly scale. We then combined gridded distributions of marine plastic density and multiplied them by the petrel UDs to map estimated exposure risk. For each map, we summed the plastic exposure risk values in all cells to provide a score representing relative estimated exposure risk. We combined maps and scores to investigate variation in exposure risk between breeding and non-breeding seasons, among populations and species, and across Exclusive Economic Zones (EEZs) and the high seas. Steps for processing and analysing the data are described in detail below and represented graphically in Supplementary Fig. 3. All data handling was carried out in R[55] and R scripts are provided, along with example data and templates[54].

A4.1. PETREL TRACKING DATA COLLATION AND PROCESSING

We collated tracking data that were collected using Global Positioning System (GPS) loggers, Platform Terminal Transmitters (PTTs) and Global Location Sensor (GLS) loggers deployed on adult petrels (Table S1; Oceanitidae, Hydrobatidae and Procellariidae). We searched for published and unpublished tracking data for all petrel species between March and August 2020, excluding the two giant petrel species

Macronectes giganteus and *M. halli* because our analyses focused on marine areas and they regularly feed on land[56]. We obtained data for 77 species (64% of the 121 target species) from the Seabird Tracking Database (www.seabirdtracking.org), ZoaTrack (www.zoatrack.org)[57], Movebank (www.movebank.org)[58], and individual researchers (represented by authors of this study or detailed in the Supplementary Acknowledgements). We collated 1,736,880 tracked locations for 7137 individuals tracked from 27 countries and Antarctica. Datasets varied in terms of number of colonies per species, and numbers of indivi- duals, years, and months tracked per population (Supplementary Data 2) and species (Supplementary Data 3).

We standardised tracking datasets to contain the following fields in the same format: latitude, longitude, datetime, species, colony name, colony latitude, colony longitude and device type. For GLS, we removed locations around the equinoxes (March equinox: −21, +7 days; September equinox: −7, +21 days) as they are unreliable[59], unless latitudes were estimated using additional information such as sea surface temperature prior to our analysis. For GPS and PTT data, we filtered locations for unrealistic speeds (>90 km/h), and visually checked maps and removed locations that were clear outliers. We removed locations within 5 km of the colony for GPS data or within 15 km of the colony for PTT data, but not for GLS locations due to large location error for these devices. We linearly interpolated and resampled GPS and PTT datasets to the sampling frequency for GLS of two locations per day.

We grouped data for each species into 148 breeding populations determined according to jurisdiction, the distance between colonies, and overlap in at-sea distributions based on the tracking data, i.e., if distributions overlapped substantially (at a 1 × 1° scale) and colonies are in close geographical proximity and in the same country, we considered colonies to belong to the same population.

A4.2. DENSITY OF TRACKED PETREL LOCATIONS

For each population, we pooled all locations for all individuals across all years by month, and then removed months with fewer than five locations. For each month, we reprojected tracked locations onto a Lambert azimuthal equal area projection centred around the geo- metric mean of all locations. We estimated kernel densities of tracked locations to compute a 95% UD, a common home-range metric, which, because the sampling frequency was standardised, represented the estimated time spent by all tracked petrels in that population within that month. We used the adehabitatHR R package[60], using a cell size of 10 km^2 and a smoothing factor of 200 km (based on the magnitude of error in estimating locations from GLS[33]). We trimmed all cells that fell over land (Natural Earth land 1:10 m polygons version 5.1.1 downloaded from www.naturalearthdata.com/) because these species do not for- age in terrestrial environments and it is extremely rare for them to travel over land, so any locations are most likely due to device error[33]. We then reprojected the resulting rasters back to a latitude and longitude projection (WGS84).

Of the 148 tracked populations, 108 (61 species) were tracked both in the breeding and non-breeding seasons. For these populations, we collated published information on the timing of breeding at a monthly scale (Supplementary Data 4) for each species or, where possible, each population. We also labelled months as breeding or non-breeding based on the tracking data. Locations were not always available for all months, with March and September often excluded from GLS datasets due to the uncertainty in light-based geolocation around equinoxes. We first calculated the distance between each location at sea and the breeding colony. For each population, we calculated the mean distance from the colony for each month, and a mean of those monthly means. If the mean for a month was greater than the population-specific mean across all months or if no individuals travelled within 200 km (chosen due to the approximate 200 km error common when using GLS devices) of the colony, this month was classified as non-breeding. To ensure there was only one breeding and one non-breeding season, if the classification of one month differed from the previous and following months, it was re- classified. We used published values except in cases when a month was labelled as breeding, but the tracking data showed that the subset of tracked birds did not attend the colony during that month, in which case, we used the label identified by the distance-to-colony method. Breeding and non-breeding months, therefore, do not necessarily represent the general phenology of the species, but instead reflect the behaviour (distance from the colony) of the majority of tracked individuals in that month. A sensitivity analysis showed that plastic exposure risk scores calculated using published breeding schedules were highly correlated with those estimated using the tracking data, Kendall's tau = 0.98 ($z = 13.879$, $p < 0.001$) for the breeding season, and tau = 0.97 ($z = 10.810$, $p < 0.001$) for the non-breeding season.

A4.3. PLASTIC DENSITY DISTRIBUTION

We used estimated global marine plastic density (count per km^2) in 1 × 1° grid cells, from publicly available outputs from three published Lagrangian particle tracking models (Maximenko[34], Lebreton[9], and van Sebille[6]). The model estimates combined floating micro and macro-plastics from ~0.333 mm to 40 cm, with different size classes having similar estimated distributions[7]. Although petrels can ingest plastic flexible plastic pieces 40–60 cm long, they generally consume smaller pieces[61]. The three models estimated plastic density using records from ~12,000 surface trawls. They provided particularly good spatial coverage in the northeast Pacific, northwest Atlantic and Australian waters, but particularly poor coverage at the poles, the waters around Southeast Asia, the northwest Indian Ocean, and the South Pacific[6]. The models simulate the movement of plastic particles through multiple years and then create a static probability grid for a single timepoint (2014) based on where particles spent most time up until 2014 (equivalent to a utilisation distribution). We do not expect interannual variation in plastic distribution to be substantial in comparison to the spatial scale of between-season seabird movement because plastics travel passively, take decades to break down, and have been released throughout the study period. Each model uses the trawl data along with weather conditions, ocean circulation models, and plastic sources and sinks to inform the movement of plastic particles and predict the number of particles in each sampled and unsampled 1 × 1° grid cell. The Maximenko model assumes particles can wash ashore and originate from a uniform input across the ocean surface[34], the van Sebille model assumes no sinks for plastic and plastics originate at the coast[6], and the Lebreton model assumes no sinks for plastic and plastics are sourced from river mouths[9]. None of the models incorporate sinking through the water column[52], ingestion by marine organisms[1], or fragmentation processes. For each ocean basin and model, a prediction value was compared to observed plastic counts, providing regression coefficients used to scale the model plastics distribution and predict plastic concentrations within all cells[6]. Each model represents observed ocean plastic concentrations well[6], with observations generally falling within 1–2 orders of magnitude around the model estimate. Further details on the methods used to model plastic density, including on how regression coefficients were used and validated, are provided in Maximenko et al.[34], Lebreton et al.[9], and van Sebille et al.[6]. Despite the variation in sampling effort, the model outputs generally agree with subsequent surveys in the Mediterranean[62], southeast Pacific[63] and southeast Asia[50].

We took the geometric mean (as opposed to the arithmetic mean) of the Maximenko[34], Lebreton[9], and van Sebille[6] models to avoid bias in our plastic density layer toward the highest estimate from any individual model because the models have log scale variability between their estimates. Additionally, because the ocean is in constant flux, concentrations at any given location are constantly changing[53], assuming a lognormal distribution of concentrations through time, the geometric mean will be a better estimate of the central tendency and closer to the median concentration than the arithmetic mean[64]. The model outputs varied in spatial coverage in coastal and polar regions (Supplementary Fig. 4), and when one of the models did not have an estimate within a cell, we used the geometric mean of the other models, or the estimate from the only available model. If there was no estimate from any model, this was marked as NA, which occurred mostly in the Arctic and the Antarctic, and in some coastal areas where the marine area was less than the 1 × 1° grid size. The model outputs were centred around 180°E. Values in cells at 0–1°W were incorrectly estimated so these were imputed from the mean values in the three adjacent cells east and west (177–180°E and 1–4°W).

A4.4. PLASTIC EXPOSURE RISK SCORES

We aggregated the monthly 10 × 10 km petrel 95% UDs for each population[33] onto the same 1 × 1° global grid of the plastic density data. All petrel UDs and the plastic density grid were divided by the respective cumulative sum for each grid so that the values of each entire raster grid summed to one. We estimated exposure risk as the mathematical product of the petrel and the plastic values in each grid cell[14]. This gives equal weight to the number of plastic pieces in each cell and the density estimate for bird tracking locations in each cell. We assume that estimated density of bird tracking locations at equal time intervals is strongly related to the time spent at risk of exposure to plastic debris, because areas where seabirds spend more time are very likely to be where foraging is concentrated[65], as a result of area- restricted searching behaviour[66–68]. We then summed all cell values and multiplied all scores by 1,000,000 to reduce the number of decimal places to produce a single score for that month (ranging from 0.0007 to 1091). For comparison, we calculated a theoretical score of 15.3, which represents what the exposure risk score would be for any species if all global grid cells contained the mean plastic density (i.e., assuming that plastic was evenly distributed across the world's oceans). We combined monthly grids to produce grids for each population, breeding or non-breeding season (if data were available for non-breeding months) and species. Scores for each population are the mean of all tracked months, and scores for each season are the mean of all months in that season (Supplementary Data 5). We used the mean to allow comparison between species with different numbers of tracked months. Maps for most populations are in Supplementary Fig. 5. For the 33 species for which we had multiple tracked populations, we searched for published population estimates (Supplementary Data 6). We calculated species-level scores as the mean of scores for each population weighted by the population size and multiplied by 0.5 if the population was only tracked during the breeding season (Supplementary Data 7).

We tested how robust our results were in relation to population size estimates, sampling frequency and tracking year. Population estimates for some species have large uncertainty, so we tested the correlation between species-level scores calculated with and without weighting by population size using Kendall's tau because scores are not normally distributed. They were highly correlated (tau = 0.83; $T = 483$, $p <$ 0.001), so our results are unlikely to be affected by uncertainty in population size estimates.

To investigate possible effects of sampling frequency, we reprocessed the tracking data without subsampling all datasets to 12-hourly intervals. We identified 44 populations for which all data were derived from GPS or PTT devices. For each track, we calculated the median interval between successive locations and recorded the maximum median for each population, and if this was less than 6 h, we regularised tracking locations at that frequency (intervals ranging from 1 min to 5 h, median = 1 h, mean = 82 min). We performed kernel density estimation with the higher-frequency datasets using a smaller 50 km smoothing factor[33] for the remaining 39 populations and used them to calculate exposure risk scores for each population. The scores estimated using the higher and lower resolution data were highly correlated (tau =

0.90, $T = 703$, $p < 0.001$), so we conclude that 12-hour sampling intervals and 200 km smoothing parameter are sufficient for a study of this scale.

Birds were tracked between 1995 and 2020 with a mean tracking year of 2012. Among the 148 populations, 139 (94%) were tracked within 5 years of 2014 (2009–2019), the year for which plastic density was estimated. Given petrels are long-lived and generally faithful to breeding sites[69] and foraging areas during both breeding and non- breeding seasons[70–73], we assumed that distributions were unlikely to vary substantially across the study period. Data on long-term trends in plastic ingestion by seabirds have not shown substantial increases during the study period[27,74,75]. A subset of 13 populations had been tracked with geolocators for the same set of months across more than three years (Supplementary Fig. 2). For these, we calculated an expo-sure risk score for each year and then tested the effect of population and year using a generalised linear model with a Gamma distribution (due to positive continuous right-skewed response variable). We checked model fit by simulating residuals using the DHARMa R package[76].

We recorded the most recent IUCN Red List assessment threat category[77], where 36 species were Least Concern (LC), 9 Near Threatened (NT), 16 Vulnerable (VU), 10 Endangered (EN) and 6 Critically Endangered (CR). Red List status categories from the year each species was first tracked remained the same for 71 of the 77 species, and we used the most recent assessment for the 6 species for which changes have occurred. Three were genuine changes relating to altered threats or conservation action (Westland petrel *Procellaria westlandica* from VU in 2016 to EN in 2017; Chatham petrel from CR in 2008 to EN in 2009 to VU in 2015; yelkouan shearwater from LC in 2004 to NT in 2008 to VU in 2012), while three were not genuine changes because they related to improved evidence for assessment (flesh-footed shearwater from LC in 2012 to NT in 2016; streaked shearwater from LC in 2012 to NT in 2015; spectacled petrel from CR in 2005 to VU in 2007)[77,78]. We calculated the proportion of the total of all exposure risk scores attributed to species in each threat category.

A4.5. SPATIAL PATTERNS IN PLASTIC EXPOSURE RISK

We used the ranked species scores to identify global-scale high - exposure risk areas by recording the region in which each species had the highest scores. We created an all-species map by summing results for each species, with those tracked in both breeding and non- breeding seasons given a weight of 1, while the 16 species that were tracked only in the breeding season were given a weight of 0.5 to avoid undue bias towards breeding colonies. We also divided the all-species distribution grid by the cumulative sum so that all values sum to one and multiplied this by the plastic density grid to produce an exposure risk map. We then overlapped this all-species map with EEZs and the high seas, obtained as an open-source polygon layer[79]. Because national jurisdictions in the Mediterranean are not yet clearly defined or are subject to dispute, we used theoretical EEZs, which are defined as 200 nautical miles from the coastline or the median point between two coastlines unless treaties and agreements have been submitted to the UN[80]. We calculated the proportion of the global risk of exposure to plastic for all petrels in each EEZ/theoretical EEZ and in the high seas. For joint regimes and overlapping claims, the score was divided evenly between the involved sovereigns. To record the links between the breeding country and the jurisdictions of plastic exposure risk, we calculated the proportion of plastic exposure risk for each population by country in each EEZ/theoretical EEZ and in the high seas[11] (Supplementary Data 1).

A4.6. SPATIAL COVERAGE AND RESEARCH PRIORITIES

To assess spatial coverage and identify research priorities for tracked species, we compared the distribution of the tracking data for each species with the estimated range maps[77]. We assessed whether major populations (>1% of the global population or 200 pairs) of each tracked petrel species were missing from any of 10 major ocean areas (NW/NE/ SW/SE Atlantic, NW/NE/SW/SE Pacific, Indian or Southern Oceans) according to the SeaVoX Salt and Fresh Water Body Gazetteer (https://www.marineregions.org/). Our tracking data covered all ocean regions within the published estimated ranges of 54 of the 77 species considered (70%). Our data compilation also revealed the main gaps in coverage for the remaining 23 species (Supplementary Table 2).

To identify research priorities for high exposure risk areas identified in this study, we used range maps to identify species or populations for which tracking data were not included in this study, but range maps indicated they may overlap (Supplementary Table 3). We recorded ingestion frequency of occurrence as the percentage of individuals found to contain plastic and the number examined as reported in Kühn & van Franeker[1]. We also carried out this process for areas for which plastic density is high and range maps showed that petrel species may use these areas, but no tracking data were available for our study (Supplementary Table 4).

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ANNEX B: SUPPLEMENTARY MATERIALS AND METHODS

CHAPTER 3

REVEALING THE FORAGING MOVEMENTS AND DIET OF THE WHITE-FACED STORM PETREL *PELAGODROMA MARINA* IN THE NE ATLANTIC

Supplementary methods 1

Two separate libraries were prepared: one to target fish and cephalopod. The following primers were selected: Chord_16S_F (5’ GATCGAGAAGACCCTRTGGAGCT 3’)/Chord_16S_R (5’ GGATTGCGCTGTTATCCCT 3’) for fish; Ceph_16S_F (5’ GACGAGAAGACCCTAWTGAGCT 3’)/ Ceph_16S_R (5’ AAATTACGCTGTTATCCCT) for cephalopods (Deagle et al 2009) – these two primer pairs were used in multiplex-; Crust_16S_F1 (5’ GACGATARGACCCTATAA 3’)/ Crust_16S_R1 (5’ TCTGTTATCCCTARAG 3’) for crustaceans (Waap 2015). Primers included the Illumina sequencing primer sequences attached to their 5’ ends.

The blocking primer to prevent host DNA amplification was designed by AllGenetics based on 16S sequences from GenBank of Pelagodroma marina, Hydrobates leucorhoa and Puffinus lherminieri using Geneious 11.1.5 and following Vestheim and Jarman (2008): 5’ CCTGTGGAACTTAAAAATYARCGRCCAC 3’. A C3 CPG spacer was added to the 3’ end of the blocking primer to prevent elongation.

DNA was amplified with a 2-step PCR approach. PCRs were carried out with 1.25 µL of template DNA, 0.2 µM of each primer, blocking primer (20:1), 2x Qiagen Multiplex PCR Master Mix and ultrapure water to a final volume of 12.5 µL.

The thermocycling conditions of the first-step PCR for fish/cephalopod primers were 15 min at 95ºC, followed by 35 cycles at 94ºC for 30 s, 57ºC for 90 s and 72ºC for 60 s, with a final extension step at 60ºC for 30 min. The thermal cycling conditions for crustaceans were the same except for 60ºC as annealing temperature and a final extension at 72ºC for 2 min.

A negative control with no DNA was included in every PCR round to check for contamination during library preparation. Oligonucleotide indices were attached in the second PCR with identical conditions and using 2 μL of the first-step product as template. The thermocycling conditions were adjusted to only 5 cycles and 60ºC as annealing temperature for fish/cephalopod. For crustaceans, the number of cycles was adjusted to 15 (94ºC for 30 s, 60ºC for 90 s and 72ºC for 90 s) with a final extension at 72ºC for 7 min.

Libraries were purified with Mag-Bind RXNPure Plus magnetic beads (Omega Biotek), pooled in equimolar amounts, and sequenced in two separate runs in 1 GB of NovaSeq PE250 (Illumina).

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Supplementary methods 2

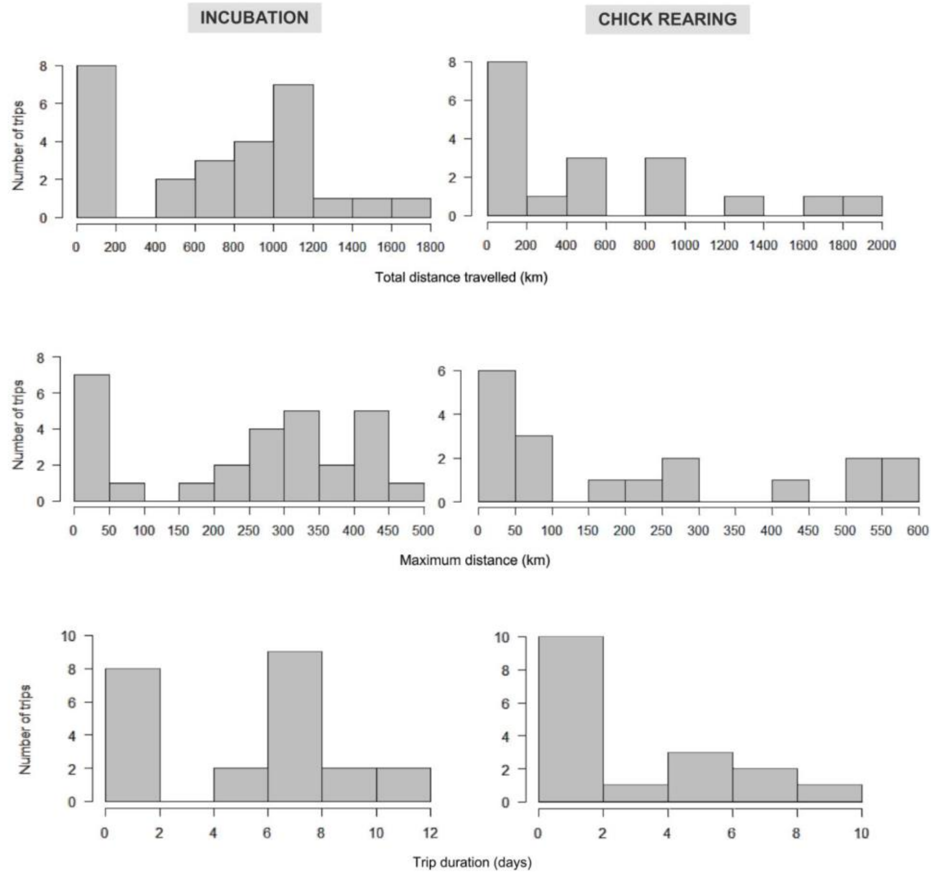

Fig. B1 Frequency distribution of the total distance travelled (km), maximum distance (km) and trip duration (days) of White-faced Storm Petrel during incubation (2018 and 2019 breeding seasons) and chick rearing (2019)

ANNEX C: SUPPLEMENTARY MATERIALS AND METHODS

CHAPTER 4

CHARACTERIZATION OF AN EXTINCT SEABIRD COLONY ON THE ISLAND OF SANTA LUZIA (CABO VERDE) AND ITS POTENTIAL FOR FUTURE RECOLONIZATIONS

Table C1 Species abundance in terms of NISP (number of identified specimens) and MNI (minimum numbers of individuals) of each identified species from the bird bone assemblage collected in the supplementary sampling points within and outside the study area. The frequency of occurrence (FO) is represented by the number of points in which a specific seabird species was found in relation to the total number of points. Numeric frequency (NF) is represented by the number of individuals of a species in relation to the total number of individuals found.

Species	NISP	Most abundant anatomic element (NISP)	2nd most abundant anatomic element (NISP)	MNI	MNI per point of occurrence (Mean ± SD; range; N)	FO (%) (38)	NF (%) (340)
White-faced storm-petrel	812	Tarsometatarsus (499)	Tibiotarsus (313)	273	13.7 ± 14.4 (1-65; 20)	52.6%	80.3%
Boyd's shearwater	96	Humerus (94)	Tibiotarsus (2)	64	4 ± 3.2 (1-11; 16)	42.1%	18.8%
Cape Verde storm-petrel	3	Humerus (2)	Tarsometatarsus (1)	3	1.5 ± 0.7 (1-2; 2)	5.3%	0.9%

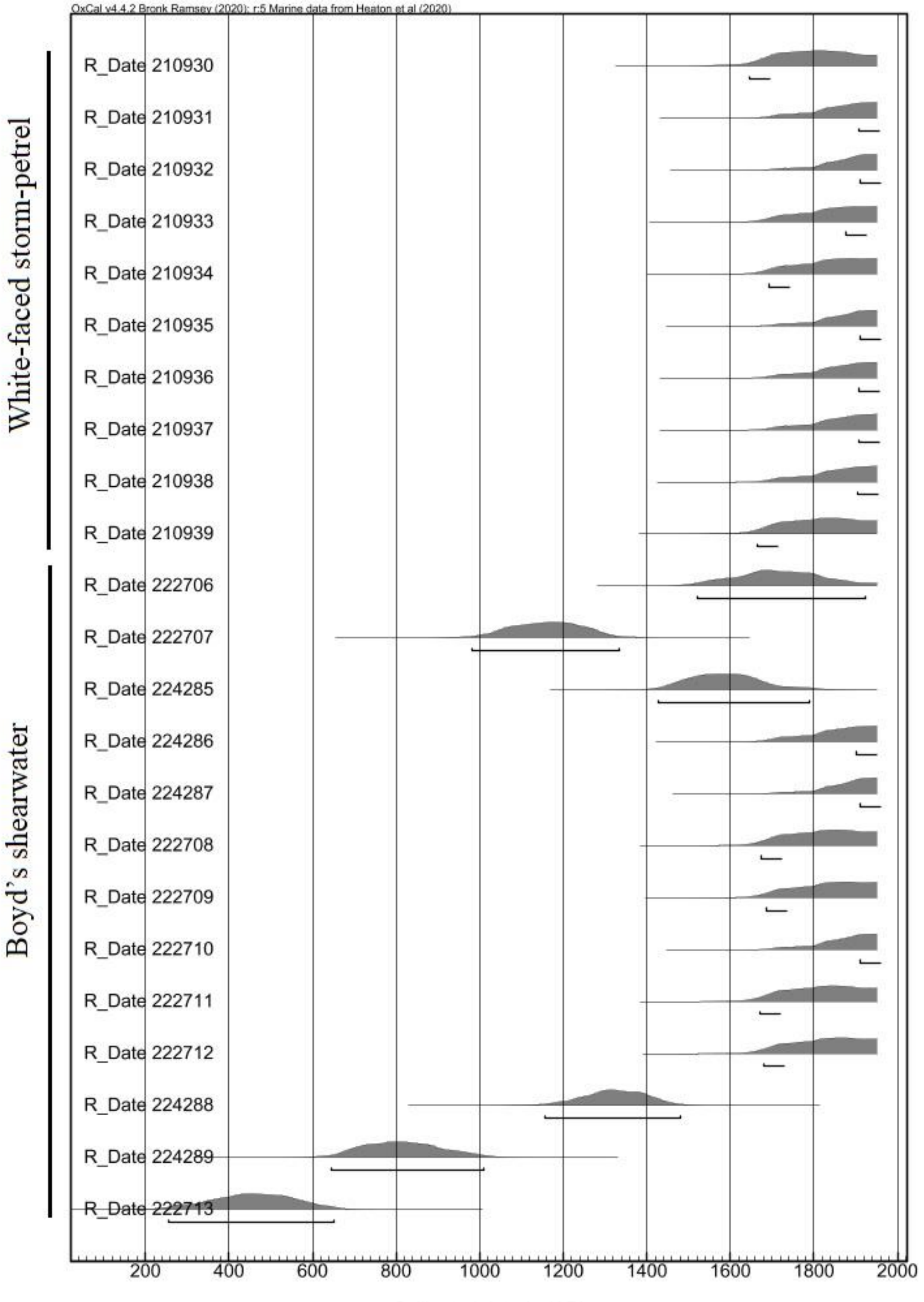

Fig. C1 Calibrated AMS radiocarbon dates of bones of White-faced storm-petrel *Pelagodroma marina* and Boyd's shearwater *Puffinus lherminieri boydi* from Santa Luzia island, Cape Verde.