



Centre d'Études
Biologiques de
Chizé



Université Pierre et Marie Curie - UFR 918, Ecole Doctorale,
Sciences de La Nature et de L'Homme : Evolution et Ecologie

Foraging ecology and breeding biology of Wedge-tailed shearwater (*Puffinus pacificus*) and Tropical shearwater (*Puffinus bailloni*) on Aride Island Nature Reserve, Seychelles: tools for conservation

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Defended the 18th December 2015

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Acknowledgements

During this long and winding path I met many people and organizations that I would like to thank, whether for their physical, psychological, financial or scientific help.

I start from the Seychelles, where it all begun. I would like to thank all the volunteers and staff members that contributed, even if with only a few hours, to the nocturnal and diurnal field work during the Shearwater's project. In particular: Gwen Maggs, Melinda Curran and Roland Duval (Assistant Conservation Officers), Alex Underwood and Uzice Samedi (Island Managers), Juan Michel, Clifford Bresson, Anselm Barra, Jim Uzice, Shannon Adeline, Rodney Maria, Elvis Bristol (Conservation Rangers), Ian Bullok, Gill Lewis, Adam Moolna, Elizabeth Atchoi, Joao Lagoa, Sabine Laukamm, Agnes Wagner, Andrew Murray, Rebecca Melville, Daniel Turner, Sieglinde Fink, Heike Szmotka, Kat Machine, Rachel Kwok, Darrah Murphy, Romain All, Victor B., Lisa Fontanesi, Yuri Bukur (Volunteers), Javier Cotin, Susan Ansel and Russel Thompson (collaborators and friends). All these people did not only contributed to the field work but also gave me the opportunity to exchange different cultural points of view and to discover the world even saying still in a tiny island in the Indian Ocean. In a small community we shared everything, joy, pain, work, but especially love for nature and the willingness to do something for conservation. I really appreciated your help guys, but also the barbeques, the fishing trips, the gardening and the life together, that, even if very hard sometimes, was worth experiencing.

Seychelles is also the base of the Island Conservation Society, the NGO that employed me for 5 years and that allowed me to complete my PhD in France. I would like to thank all its members in particular James Cadbury (Chairman ICS UK), Adrian Skerrett (Chairman), Alice Mascarenhas, Ahab Downer, Adam Moolna (CEOs), Pierre André Adam (Projects & Science Manager) and Dixon Bastienne (Finance & Administration Manager) from the Mahe head office. The ICS trustees and the scientific committee, for interesting and useful scientific exchanges. Of course, Thanks to the 100 birds that had to be manipulated and equipped with weird things at their legs..sorry guys..just think it's for the good of the species!

Out of Seychelles I thank the co-founders of the shearwater project: FONDATION TOTAL (in particular Mme Laure Fournier), James Cadbury Foundation (UK), Miguel Torres (SP) and the Centre d'Etude Biologique de Chizé (FR).

In particular I would like to thank all the administrative and technical CEBC staff. Delphine Bonnet, Annie Telias for dealing with the administration related to my settlement at Chizé and Stephanie Dano for the birds' sexing.

Toujour en Chizé j'ai rencontré beaucoup des gens que non seulement m'a appris le français (plus ou moins) mais que m'a accompagné sur la route de mon dernier année de thèse. Je parle notamment de mes copines de bureau et de thèse Carine, Adriana, Cécile, Laura, avec qui j'ai partagé la joie et la douleur de la thèse. Merci aux les autres pots du labo : Almut (thanks for the carriage trips!), Edo, Thomas, Alicia, Gaëtane, Louis, Paul, Marie, Heloise et Julien, pour m'avoir fait sentir partie d'un group!

Bien sûr un grand merci à mes colloques, Kévin, Mathieu, Alexis, Romain, Gildas et Cécile, pour m'avoir fait sentir à la maison!

I would also thank all my worldwide collaborators: Jacopo Cecere, Anne-Sophie Bonnet-Lebrun, Kévin Le Rest. Thanks for the scientific enrichment our collaboration have

brought and can still bring. A special thanks to my official english corrector Alexander Coles, for supporting me during the last part of the path, until the end.

Talking about science I reserve a special thank to my directeur de thèse Vincent, co-directeur Gerard and co-encadrant Andrés. For your useful thoughts and for giving me the opportunity of being here now.

Dulcis infundo, finalmente posso scrivere in una lingua che posso autocorreggermi da sola.. vorrei ringraziare tutti gli amici che, pur da lontano mi hanno supportato moralmente per tutto il percorso della tesi e anche, perché no, della vita. Chiedo scusa se sono mancata a matrimoni e battesimi, c'ero sempre.. con la mente! Grazie agli avventurosi che hanno condiviso con me la vita su Aride: Attilio, Greta, Franz, Tonno, Renato, Alessandro e Luca. Che nonostante il mare in burrasca e i cappottamenti sono venuti a darmi supporto morale e lavorativo quando ne avevo piu' bisogno! Grazie agli amici del bar Cristina e Beppe, che restano comunque un punto di riferimento per ogni ritorno. Grazie alle amiche di sempre Katia e Sara, con cui sono cresciuta e che é sempre un piacere incontrare tra un viaggio e l'altro. Grazie alla Faby, perché anche se non leggerai queste righe, so che ci sei da qualche parte e che vegli su di noi; un giorno ci rivedremo.

Gli ultimi, ma infatti i primi, i miei genitori, mio fratello e mia nonna, perché mi hanno sempre aiutato ed incoraggiato a seguire i miei sogni ed hanno sopportato la follia e la lontananza senza farcele pesare. Grazie mamma e papà per avermi fatto..senza di voi non sarei qui!

Ah, yes, thanks to the music...to keep me sane!

Résumé en Français

Les extinctions d'espèces et les menaces dues à l'augmentation de la pression anthropique ont augmenté très vite surtout après la 2ème guerre mondiale. En conséquence le concept de conservation de la nature s'est développé et est devenu une science pluridisciplinaire, dans le monde entier, au service de la protection des espèces menacées. Si au départ les efforts de conservation ont été prioritairement orientés vers les espèces en danger critique d'extinction afin d'éviter leur disparition, on constate plus récemment, l'émergence de recherches et de développements technologiques sur une plus large diversité d'espèces et d'écosystèmes. Les procellariiformes constituent un ordre d'oiseau parmi les plus menacés dans le monde, avec 45% de leurs espèces en danger d'extinction; néanmoins certaines espèces restent peu étudiées. Cette étude se focalise ainsi sur l'analyse de la quasi-totalité du cycle de vie de deux espèces de puffins sympatriques; le puffin tropical (*Puffinus bailloni*, PT) et le puffin du Pacifique (*P. pacificus*, PP) nichant tout deux sur la réserve naturelle d'Aride Island (Seychelles). L'objectif est de mieux comprendre les interactions existantes entre ces espèces, ainsi que l'influence de l'environnement, au sein de la colonie et dans le milieu marin.

Ces analyses ont permis de déterminer les effectifs, la distribution des individus, le succès reproducteur et la sélection d'habitat au sein de la colonie, ainsi que d'évaluer la distribution des individus et la sélection d'habitat en mer (grâce à la pause de balises GPS et GLS). Les résultats du recensement ont permis d'estimer le nombre de couples à 15,000 pour le PP et 30,000 pour le PT (où la population est probablement en déclin). Les deux espèces sélectionnent ainsi davantage des zones escarpées avec des végétations basses. Les PP montrent également une préférence pour les zones rocheuses avec un sol profond. Les PT nichent pendant toute l'année mais de manière plus intensive en fin de saison de reproduction des PP et le taux d'échec de la reproduction est maximal durant la période où les deux espèces nichent en même temps. Dans le milieu marin, on observe une ségrégation spatiale entre les deux espèces, exploitant des zones d'alimentation bien distinctes hors saison de reproduction et se distinguant également dans leur comportement alimentaire. En effet, les PT peuvent plonger jusqu'à une profondeur de 16 mètres, contrairement aux PP qui ne plongent pas et capturent leurs proies proche de la surface. Grâce aux données de distribution en mer, il a ainsi été possible de déterminer les caractéristiques océanographiques sélectionnées par les deux espèces et de réaliser des cartes d'habitats potentiels. Hors de la saison de reproduction, les PP se déplacent sur toute la partie tropicale de l'Océan Indien et sélectionnent des zones profondes loin des côtes et avec faible concentration de chlorophylle; tandis que pendant la saison de reproduction ils sont davantage associés à certaines caractéristiques océanographiques particulières, comme par exemple de zones d'upwelling générées par de fortes différences de bathymétrie. Les PT sélectionnent quasiment les mêmes caractéristiques pendant et hors période de reproduction mais se déplacent plutôt vers l'archipel des Comores et la Somalie. Les deux espèces sont aussi associées à des prédateurs de sub-surface, notamment le thon.

Dans la colonie les deux espèces peuvent être en concurrence sur le site de reproduction mais les PP semblent être de meilleurs compétiteurs. En mer les deux espèces, bien qu'elles se nourrissent des mêmes proies, elles s'alimentent dans des zones bien distinctes ce qui entraîne une forte ségrégation spatiale. Concernant les perspectives de gestion, nous proposons la mise en place de mesures de conservation pour les deux espèces, mais favorisant spécialement les PT et nous recommandons de veiller à une gestion durable des ressources de thon dans l'EEZ des Seychelles.

English Summary

Species extinctions and the threats caused by humans activities increased rapidly after the Second World War. As a consequence, Conservation biology developed as a multidisciplinary science and conservation-oriented research and conservation actions increased all over the world. At the beginning, conservation efforts were mainly directed towards rare and endemic species in order to avoid their extinction. Lately, following the opportunity to carry out more sophisticated research, more categories were taken into account at ecosystem level. With 45% of its species threatened with extinction, the procellariiformes are one of the most endangered orders in the world. Moreover, information on population estimates, trends, movements at sea and population dynamics are lacking for many species. Here we investigated almost the full life cycle of two sympatric species of shearwaters, the tropical (*Puffinus bailloni*) and the wedge-tailed shearwater (*P. pacificus*), both breeding at Aride Island Nature Reserve (Seychelles), in order to analyse their interactions both at sea and in the colony. We first assessed the habitat selection, abundance, distribution and breeding success of the two species at the colony. Then, we created habitat suitability maps at sea based on birds' movements during the breeding and inter-breeding seasons. The breeding population consisted of c. 15,000 and 30,000 breeding pairs for wedge-tailed and tropical respectively, the later probably declining. These two species share the same breeding areas and differ slightly in habitat selection at the colony. Both species selected steep and lowly vegetated areas, while the wedge-tailed also selected rocky areas with deep soil. The tropical shearwater nests year-round, however it seems to have a peak of breeding at the end of the wedge-tailed breeding season and its failure rate is slightly higher when the two species co-exist. At sea, the foraging behaviour during chick-rearing differs strongly because the tropical shearwater dives up to 16 m while the wedge-tailed behaves as a surface feeder. Finally, during the inter-breeding period, both species select the same habitat features but the areas that they exploit hardly overlap. Thanks to the use of geolocators and GPS it has been possible to determine the oceanographic characteristics selected by the two species and to draw potential habitat maps. Outside the breeding season, the pacific shearwaters move around the whole tropical Indian Ocean, and select deep areas far from the coasts and with a low chlorophyll concentration; whereas during the breeding season they are more associated to certain oceanographic characteristics such as upwelling currents generated by strong bathymetric differences. Tropical shearwaters select almost the same characteristics during and outside the breeding season but tend to move towards the Comores and Somali Basin. The two species are also associated to sub-surface predators, particularly tuna.

Therefore we found strong evidence of spatial, rather than ecological segregation, between the two species at sea in both foraging behaviour (diving depth) and marine areas used during inter-breeding season. On land, they are likely to compete for breeding sites as their options for suitable nesting sites are limited, with the wedge-tailed often over competing the tropical shearwater. Hence, we propose conservation measures for both species but favouring more particularly the tropical shearwater.

CHAPTER 1

1.1 General Introduction

The “anthropocene”: an extinction era

At present, human beings are considered the dominant species on Earth (Vitousek et al. 1997). Anthropogenic actions can modify entire ecosystems and lead to the disappearance of the most vulnerable species and the less resilient communities (Peterson et al. 1998; Hoegh-Guldberg 2011). The negative impact of human beings is positively correlated to the humanity development (Steffen et al. 2011) and it started already in early history with the first appearance of *Homo sapiens* throughout the continents. In fact, first the change in climate and then the arrival of humans were most probably the cause of the late Quaternary megafaunal extinction (Prescott et al. 2012). However, anthropogenic actions started to deeply modify the planet with the XIX century industrial revolution and they grew exponentially after the World War II, a phase called by scientists “Great Acceleration” (Steffen et al. 2011). The first half of the XX century saw indeed at least 70 known species extinctions according to Cragg (1968a). However, to quantify the exact number of extinctions, information on the total number of species present on earth is necessary, a data which is at present still unknown (Wilson 1988). In any case, it is clear that human beings have been responsible for what is called the 6th mass extinction (Ceballos et al. 2015).

This long, and still ongoing, chain of extinctions was triggered and powered by the human perception of natural environments. In fact, since the human development begun, natural ecosystems and habitats were only seen like an unlimited resource, something to be fully exploited and that will never end. The idea of sustainable harvest lasted only in very isolated and rural community while the rest of the world started to produce and consume at a quick pace. Since the “Great Acceleration” started, the examples of vertebrate extinctions are many. The areas more threatened by extinctions are inevitably the most rich in biodiversity. It has been estimated that the number of species of a particular group of organisms in an island system (or habitat island) increases approximately as the fourth root of the land area (Wilson 1988). This calculation can help to estimate the biodiversity loss in many habitats. For example, the tropical world is heading towards an extreme reduction and fragmentation of tropical forests, a major hotspot for biodiversity.

Habitat fragmentation increases the insularity syndrome and some species – particularly the large ones that need greater extensions of territory – end up disappearing (Mc Arthur & Wilson 1967; Blondel 1986; Whittaker & Fernández-Palacios 2007). If the reduction of tropical forests continues at this pace it will be accompanied by a massive extinction of species (Wilson 1988; Brooks et al. 2002). The basic models of island biogeography are particularly suited to tropical forests as tropical species are more localized than the temperate ones (Helmus et al. 2014). Then, even if a portion of the species survives, these will probably have suffered significant reduction in genetic variation (Wilson 1998, (Helmus et al. 2014). For example three patches of subtropical forest in Brazil, varying from 0.2 to 14 square kilometers, were isolated by agricultural

clearing for 100 years and their resident bird species suffered a 14 to 62% extinction rate (Willis 1979).

There are many other examples of extinctions, especially in islands hosting rare endemic or native species never exposed to predation pressure. These species are considered particularly vulnerable either because they are flightless birds, or/and because they have evolved in the absence of predators and have no defences against them (Milberg & Tyrberg 1993).

The biodiversity of the small islands in the Pacific and Indian Oceans started to be significantly affected by anthropogenic factors much earlier than its continental counterpart, after the beginning of the European maritime expansion in 1400. Island extinctions after 1600 are well documented and in many cases bird species have been lost from single islands or have become globally extinct as a result (Milberg and Tyrberg 1993). It is important to underline that ninety percent of the c.108 species thought to have become extinct since 1600 were restricted to islands (Johnson & Stattersfield 1990).

The most famous example of islands extinctions is the case of the Dodo (*Raphus cucullatus*), a flightless bird living in the uninhabited island of Mauritius (Indian Ocean). When the firsts Dutch settlements started to widespread in 1638, the interference of introduced foreign animals (mainly cats and rats) together with the continued overuse of the birds for food led to their total extinction by the end of the century (Cheke & Hume 2008). But not only flightless land birds were affected by humans' arrival in small islands. Procellariidae and Columbidae are the most frequent orders among the extirpations of island populations, based on fossil recoveries and historical evidences (Milberg & Tyrberg 1993). In fact, many seabird species that were breeding undisturbed in many oceanic islands have been extirpated or have become globally extinct after the arrival of humans. For some species,, the only elements documenting their presence are fossil evidences (Milberg and Tyrberg 1993). It is the case of two species of petrels (*Pterodroma rupinarum* and *Bulweria bifax*) breeding at St. Helena (to UK), which became extinct after humans colonized this island in 1502 (BirdLife international 2012). In general, the major anthropogenic factors affecting biodiversity are notoriously: habitat loss and fragmentation, introduced invasive species, pollution, overharvest, and lately the climate change (Mills 2012).

Conservation biology: definition and development

Although species declines and extinctions caused by humans started already in 1400 and intensified in 1800 (as documented above), awareness and willingness of the scientific community and the general public to protect natural ecosystems and species is a fairly recent feeling (Pfeffer et al. 2001).

As the cases of population reduction and species loss were increasing, around the years 1940s and 1950s conservation thoughts started to emerge. The first minds emerged as an "aesthetic concern for wilderness", and when ecological studies and the concept of ecosystem started to develop, this "romantic era" became a more science-based movement known as conservation science (Cragg 1968). Since the beginning, conservation biology required a multidisciplinary approach, which involved social and cultural studies (Cragg, 1968b). The foundation of the International Union for the Conservation of Nature (IUCN) in 1948 and of its financial supporter the World Wild Fund for Nature (WWF) in 1961 can be considered as the starting point of the modern conservation awareness. At the beginning, the operations of the IUCN were mainly about

exposing problems and persuading people, and the focus was on the species particularly closed to extinction (IUCN Red List). Nature was still very much seen as a benefit for human kind in an economic prospective (Cragg 1968a) but more protectionist thoughts started to emerge.

Dasmann in 1968 and Erenfeld in 1970 introduced the concept of conservation biology. This new discipline was then described by Soulé (1985) as “a new synthetic discipline addressing the dynamics and problems of perturbed species, communities and ecosystems” and with time it became a multidisciplinary science developed to address the loss of biological diversity (Hunter 1996; Meffe 2006; van Dake 2008).

After years of research the main goals of conservation biology have evolved and became: first to evaluate human impact on biological diversity and second to develop practical approaches to prevent the extinction of species (Soulé 1985; Wilson 1999). Conservation biology was described as a “mission-orientated crisis discipline”. In fact, in order to address pressing problems, conservationists have often to act fast without being completely comfortable with the theoretical and empirical bases of the analysis. Therefore tolerating uncertainty is often necessary although the principle of precaution needs to prevail.

According to Soulé (1985) conservation biology is supported by strong postulates both functional and normative. The functional postulates suggest the rules of action in order to maintain both, form and function of natural biological systems. They follow evolutionary, ecological, demographic and spatial rules regulating the ecosystem functioning and they need to be followed in order to achieve the subsistence of natural ecosystems. The normative postulates are value statements that create the ethic basis towards other forms of life. They cannot be tested or proven completely, but they provide the ethic upon which conservation decisions should be made.

After the milestone publication of Soulé (1985), that gives the basic definition and aim of conservation biology, other authors have enriched this new emerging discipline based on the experience accumulated during the firsts two decades of experiences in this field. It was in fact only after ten years from the definition of conservation biology that Caughley (1994) implemented this discipline with some important directions driven by the two major paradigms.

The first is the small-population paradigm, it has a mainly theoretical approach and it is the center of all conservation actions carried out during the 1980s. It is centered on the notion that small populations are at major risk of extinction than big ones. In fact, a small number of individuals can lead to genetic and population dynamic problems, which in turn can bring the population into the extinction vortex (inbreeding depression combined with demographic stochasticity and genetic drift) (Lynch et al. 1995; Masel 2011).

The second paradigm addresses population decline and focuses on means for detecting, diagnosing and stopping it. This paradigm has a pragmatic origin and it is rooted in practical examples. It states that population declines have always one or more tangible causes that can be defeated with appropriate skills. It is therefore applicable mostly on a case-by-case basis and it lacks of a proper theory. Within this paradigm, four main agents of populations decline (called the “evil quartet”) can be identified: overkill, habitat destruction and degradation, impact of introduced species and chains of extinction (Pullin 2010).

However, to identify the real cause of a population decline, it is extremely important to gain as much knowledge as possible about the species in object (ecology, context and status), then different causes can be listed and an experiment is required to identify the

real cause (Martin et al. 2012; Pullin 2010). These steps are fundamental in conservation biology when management is required to stop species decline. Most importantly, faulty or not informed recommendations can have, in conservation, the opposite result and lead to the extinction of a species. The exploratory and scientific processes are therefore fundamental to make informed and correct conservation management decisions.

At present, conservation biology is still strongly based on these basic concepts even if it has been enriched with other disciplines such as ecology, taxonomy, demography and genetics. These sciences theories are integrated in conservation policies and they can be directly implicated in the management of species and ecosystems, captive breeding and reintroduction, population genetic analyses and habitat restoration (Buchholz 2007; Fryxell et al. 2014).

With the development of the conservation biology concept, wildlife management started to mutate and evolve. In fact, if at the beginning it was only seen as management towards human benefits, but then it became more connected to species and ecosystem conservation approach. In this regard Fryxell et al. (2014) underline how, until about 25 years ago, “wildlife” was synonymous with “game” and it was often hunted for sport. Even if the management of “game animals” still exists, population management has also developed towards the conservation of endangered or declining species.

Some recent conservation debates

As conservation biology and management developed and evolved as a science and discipline, a different numbers of debates developed with them.

a) The “new conservation” debate

The controversial argument between human development and species survival became aglow when a “new conservation” concept was developed by Kareiva and Mavrić in 2012. In their “re-visitation” of the Soulé essay on the basic concepts of conservation biology (1985), the authors re-organized such concepts with a more contemporary view defining the “new conservation science”. This new movement is supported by scientists like P. Kareiva, C. Thomas, E. Marris, M. Mavrić and Lalasz (see Marris 2007; Lalasz et al. 2011; Kareiva 2012; Kareiva & Mavrić 2012; Thomas et al. 2013) who think that affection for nature will grow together with income growth. Therefore, the more people will be enriched and happy and the more they will care for conservation and nature. The new conservation science differs from conservation biology as its aim is the improvement of human well-being and biodiversity at the same time, directing the conservation efforts more towards that part of biodiversity that provide services to humanity (Kareiva et al. 2011; Kareiva & Mavrić 2012). The basic idea is that with the huge increment of human population on earth over the past 25 years (from 4.5 to 7 billion people), pristine habitats no longer exist; therefore considering humanity as part of nature becomes a necessity. This new concept brought anthropologic disciplines (i. e. economics, psychology, political science etc.) to be part of the new conservation science. Conservation has to deal with the human livelihood to act on nature, and the nature protection cannot work without the support of people. A strong collaboration with big corporations is another novelty introduced by the new conservation science that strongly differs from the first concept of conservation. Corporations are controlling most of the resources on earth, therefore it is important to deal appropriately with them and to establish a legacy aimed at both the human and nature well beings.

This new movement sees forward-looking conservation as acting primarily for the people. In other words, in a world without poverty where everybody is happy there will be more space for the support of nature and its conservation.

This concept is opposing at the classic concept of conservation that sees development and population growth as a threat for biodiversity (Wilson 2007; Soulé 2013).

It is therefore very clear how this new line of thought found the opposition of the conservationists more faithful at the first concept of conservation biology.

In fact, at the other side of the debate there are the more conservative conservationists like M. Soulé, E.O. Wilson, S. Pimm and B. Miller (see Soulé 2013; Miller et al. 2014; Pimm et al. 2014; Wilson 2007) who think the human footprint on nature is already too much and it is provoking an exponential increment of extinction rate and threats to species (Pimm et al. 2014; Ceballos et al. 2015). Therefore the first priority for conservation biology should be the whole biodiversity without distinguishing on species that are more or less worth to be saved based on their utility for humans (Doak et al. 2014). The worth of nature is not questionable and humanity has the obligation to minimize its degradation.

This debate inevitably provokes a question: what is the future for conservation?

It is of common agreement that as the world is changing rapidly, hence the discipline of conservation needs to mutate in turn, taking into account the recently fast human development (Rudd 2011; Doak et al. 2014). However, many scientists think that the new conservation science is too orientated towards the human well being and less on the conservation of biodiversity itself (Soulé 2013; Doak et al. 2014). There are no doubts on the importance of meeting human needs (Doak et al. 2014) as joint economic development and conservation programs can play an important role in meeting two objectives at the same time: human welfare and environmental conservation (Reyers et al. 2012). However, economical interests should not overshadow nature and the intrinsic value of all the species should be kept unchanged and not based on their utility for humans (Doak et al. 2014) as it is claimed by the new conservation advocates (Kareiva et al. 2007; Marvier & Wong 2012).

In general, there will never be a shortage of support for the increasing use of natural resources by humans, but there could be a lack of it for helping biodiversity to withstand the decreasing availability of space. Therefore if conservation scientists will start promoting economic prosperity as first goal, there will be no one left to stand for biodiversity and interests of nature and people will both suffer as they are closely tight together (Doak et al. 2014).

New conservation science supporters also argue about the utility of nature reserves, seeing them as an obstacle to humans' development and not particularly useful for biodiversity (Burkey 1989). However, the creation of parks, together with the innovative management of resources, have been proven to be highly beneficial to biodiversity and to have decelerated its decline (Margules & Pressey 2000; Pullin 2010; Miller et al. 2012). Without protected areas, biodiversity losses would have been greater than they have been until now (Rodrigues 2006; Hoffmann et al. 2010).

To summarize, we can see that a major challenge of conservation in the "Anthropocene" is to integrate threatened biodiversity into a heterogeneous mosaic of habitats characterized by strongly contrasting anthropogenic, biotic, and environmental conditions (Koh & Gardner 2010; Kueffer & Kaiser-Bunbury 2014).

b) The “intervention vs. leave as it is” debate in nature reserves

The debate on the new conservation science inevitably carries other minor, but still important, debates. The one involving nature reserves is definitely of interest for most of the conservation world.

For new conservation science advocates, the nature reserves are still important but conservation should not focus on them anymore as they are considered a failing attempt to save biodiversity (Kareiva et al. 2011). Instead, conservationists should focus more on areas that are highly impacted by humans (like gardens or agricultural landscapes) where biodiversity, even if in bad shape, can still survive (Marris 2011). This idea is seen as minimalist to other conservationists that perceive protected areas, when integrated into land use plans, as part of larger and connected conservation networks, which offer practical, tangible solutions to the problems of both species loss and adaptation to climate change (Lopoukhine et al 2012). The solution of concentrating in areas that can be easily accessed by people in fact seems insufficient for species that cannot survive the impact of humans and which often need large nature reserves in order to survive, i. e. the big predators (Wilcox & Murphy 1985). The persistence of these top predators is indeed indispensable to maintain the equilibrium of the ecosystem. A classic example is the one of the coyote and the birds. This study reported that the abundance of birds in 37 isolated fragments of canyon around the city of San Diego was dependent not only on the size of the undisturbed area and on the distance from another canyon fragment, but also by the amount of coyotes present in each small canyon. In fact, the coyote was acting as the top-predator, thus controlling the population of mesopredators (like cats or foxes), which predate on birds (Soulé et al. 1988). Many other examples are available on the role of top-predators on different ecosystems and on why their preservation is a priority (Boyd et al. 2006). Unfortunately, as these top predators often require vast areas to survive, they are particularly exposed to anthropogenic impact. This makes the role of nature reserves particularly important as with the aim to save one species, they can preserve the whole ecosystem.

Another important role of nature reserves is as a reservoir for species. In fact, acting on farmlands and city neighbourhoods to increase biodiversity would be useless if there were no reserves from where species can move (The state of nature conference report, 2013). Still, according to Rudd (2011), 80% of the conservation scientists believe that in a continuously changing world, professionals need to re-think conservation goals and standards of success to better address the issue of species loss. These goals should not remain within the boundaries of nature reserves (even if their value is still incommensurable) but move out to manage also semi-natural areas on a large scale (see for example Tucker et al. 1997 for Europe), and to teach conservation values to the new generations in the schools.

Therefore, many actions are required outside the boundaries of nature reserves, in order to create ecological corridors joining fragmented areas or semi-natural habitats where the more adaptable species can thrive (Rosenberg et al. 1997). Actions are often required to manage nature reserve areas as well. In fact, to allow for the existence of the most vulnerable and/or declining species, modifications on nature reserves ecosystems are often required. These actions include, among others: removal of invasive predators, vegetation rehabilitation or modification and limiting anthropogenic impacts. Actively modifying the ecosystems in reserves for conservation purposes is no easy task and it has to be deeply thought out before any action is undertaken (Sutherland 2004). Some conservationists believe that nature reserves should be left untouched to allow nature to undertake its course and in certain cases it is the best course of action (Peterken 1996).

However, some time interventions in nature reserves are required. In these cases there are few rules that need to be followed. Native key ecosystem species threatened with extinction often have priority when it comes to making management decisions. To maintain these important species' populations, control or facilitation of other species present in the ecosystem may be required, particularly on islands (i. e. invasive predators' control or vegetation restoration; see for example in Seychelles Rocamora & Henriette, 2015). However, which species to control are not always the non-native ones and the species to favour are not always the native ones. Indeed, it can be the case that a non-native species has replaced an extinct one and provides the services that the extinct species can no longer maintain, allowing the ecosystem to function (see also 'novel ecosystems'; Hobbs et al. 2009; Hobbs et al. 2013). Alternatively, a native species may need to be controlled if it is impacting a very rare, threatened or declining species. This can occur when an ecosystem is deeply disturbed and the equilibrium is lost in favour of the most opportunistic species and at the expense of the most vulnerable ones (Goodrich & Buskirk 1995).

However, before whichever management action is, or is not, undertaken, research is required on the subject- without a good understanding on the community dynamic it is impossible to make good management decisions (Fryxell et al. 2014).

The evidence-based conservation

Whichever position is taken regarding big or small debates, conservation (like any other discipline) needs evidence whenever possible to prove if a management action gave the expected outcome or not (Sutherland et al. 2004a; Sutherland 2015).

Such evidence can be examples of good or bad experiences from nature reserve/species management actions, which can inform other conservation managers' actions (Sutherland 2015).

However, to produce conservation evidence, an important amount of baseline information is required on population size, habitat selection and use, demography, species distribution and movements.

First, the knowledge of the size or density of a population is often an essential prerequisite to manage it effectively (Fryxell et al. 2014), therefore it is required to investigate whether a population is too small, too big, increasing or decreasing in order to decide if any action is required. For some cases a population index may be enough if the main aim is just to have a trend. In fact, indices provide measures of relative density and are used only for comparison purposes. More detailed information than indices may be required if information on the species is lacking, the species is suspected to be declining or if it counts a small number of individuals or populations (i. e. endemic species) or simply because it is important to know its distribution within a certain area for management purposes. Management decisions often require information on density, and/or trends in density, and many factors can drive the decision on the methods to undertake to obtain these information (Bibby et al. 2012).

Second, it has been recognized that habitat structure is fundamental in influencing its use by animals (MacArthur & MacArthur 1961). Therefore, habitat assessment is an important part of wildlife ecology. In fact, good understanding of habitat selection allows appropriate management decisions regarding different forms of land use and can improve the success in case reintroduction actions are required (Fryxell et al. 2014). Habitat use information is important during all the different stages

of a species life cycle, during breeding and non-breeding periods and for both foraging and breeding sites.

Third, describing and predicting stochastic population dynamics in time and space is fundamental to ecology and conservation biology (Lande et al. 2003). Population dynamic can be influenced by different demographic factors including social structure, life history variation caused by environmental fluctuations, dispersal in spatially heterogeneous environments and local extinction and colonisation (Lande 1988). The assessment of populations' demographic parameters is therefore very important to understand what happens within a population and identify the key stages that demography is most sensitive to, in order to guide direct management (Sutherland et al. 2004a; Bibby et al. 2012; Fryxell et al. 2014).

Finally, animal movement is directly dependent on environmental conditions (such as climate, resources, presence of partners/predators/competitors) but it is also the result of complex evolutionary mechanisms driving physiological and behavioural responses (Nathan et al. 2008). Given that, the analysis of animal movement can be used as a tool to identify such conditions and to assess the capacity of animals to respond to rapid changes in ecosystems (Urbano & Cagnacci 2014). With the use of telemetry to track animal movement, it is now possible to assess the environmental conditions favourable for a species during different stages of its life cycle and to identify/predict suitable areas. Knowledge of suitable habitat has become an important tool in conservation for both management (Gurnell 2002) and identification of threats (i. e. Arcos et al. 2012).

The nature reserve context

As underlined above, nature reserves remain a cornerstone of global conservation efforts (Lopoukhine et al. 2012). Over 100 000 protected areas have been established worldwide, covering over 12% of the Earth's land surface (based on the World Database on Protected Areas: : https://www.iucn.org/about/work/programmes/gpap_home/gpap_biodiversity/gpap_wdpa/) and representing one of the most significant human resource use allocations on the planet. The importance of protected areas is reflected in their widely accepted role as an indicator for global targets and environmental assessments (Chape et al. 2005).

However, establishing and properly managing nature reserves is not the first priority for most of the world countries, especially the developing ones. Therefore, even if a protected area is hardly instituted, it does not mean it will be well managed or it will keep its biological importance (Chape et al. 2005). The amount of funding available to a nature reserve is fundamental for its management and subsistence. A nature reserve can be managed by different entities: non-governmental organizations (NGOs), private owners or governmental bodies; in any case the managing board and legislation have the responsibility of making decisions on which actions are allowed to be undertaken within its boundaries. A nature reserve can be integral (no human activities are allowed within its borders) or, in most of the cases, a different degrees of human actions are allowed within its borders (IUCN). Integral nature reserves offer to biodiversity a refuge from disturbed areas and are often occupied by many species (Kingsland 2002).

As discussed above, management decisions are not easy to undertake especially if a nature reserve hosts many species with different levels of conservation concerns. In the "Anthropocene" the little space left for species survival has reduced with years and

human development (see above) and it is highly contended among species (Brussard and Tull 2007).

Organisms within a community interact continuously with each other (Begon et al. 1999) and they need food and shelter to improve their fitness (Krebs & Davies 2009). Therefore, the ensemble of direct and indirect competition, predation or mutualism interactions, can deeply modify and shape the whole community, driving evolutionary changes (Pianka 2011). These processes can be amplified/modified by the fact that species live in limited places. In fact the process of habitat loss and fragmentation brought by human activities did inevitably increase the inter- and intra-specific competition for both resources and breeding ground (Coppack & Pulido 2004).

In particular, interspecific competition mainly occurs when individuals of different species utilize common and limited resources (Fryxell et al 2014). Competition for limited resources can affect population size and distribution and the type of limiting resources also depends on species' life history and ecology niches (Dhondt 2012). This is particularly the case on islands, where in the absence of predators, ecosystems and communities are bottom-up regulated (Polis & Strong 1996). There are at least two groups of limiting resources: space and food. Competition, to occur, must have some effect on the fitness of both parties (Fryxell et al. 2014) but competitive effects can be unequally distributed among competitors. This is the case of asymmetric competition, when a species outcompetes the other (Begon et al. 1999).

The ecological niche concept in a competition framework

The modern concept of ecological niche was proposed by George Evelyn Hutchinson (1957) and it is defined as a quantitative n-dimensions hypervolume constructed by the range of environmental features that enable a species to maintain a viable population indefinitely (Blonder et al. 2014). Independent axes, that have a biological meaning for the species, characterize the dimensions of the niche (Maire et al. 2012). If we assume that interspecific competition does truly occur among co-existing species, the ecological niche can be divided into two categories: the fundamental niche is defined in absence of competition while the realized niche is characterized by the presence of competition among species (Hutchinson 1957, Maire et al. 2012).

Based on the principle of competitive exclusion, niche theory implicitly assumes that, in order to have a stable co-existence, niches of co-occurring species must differ (Hutchinson 1957; Chesson 1991) although a certain degree of similarity is permissible (May & Mac Arthur 1972; Pianka 1974). By measuring competitors' niche overlap it is possible to assess the effects of density-dependent competition on the tolerable upper limit of niche overlap (Young 2004). Moreover, the conceptual niche framework allows testing if competition between sympatric species is happening with the use of species assemblages modeling.

The ecological niche concept is strongly related to habitat selection (Maire et al. 2012). The latter is considered as a density dependent process. In fact, when populations are at low-density levels, individuals can freely occupy the habitat that maximizes their fitness. At the opposite, when population density levels increase, the individual fitness decreases within the most favourable habitat, making adjacent and less favourable habitats providing the same fitness. If habitat suitability can vary in function of population densities (Morris 1988), then habitat selection depends not only on resources abundance but also on the density of the same and/or different species sharing the same area. In the latter case, which is the most commonly represented, the

organization of the community can be based on shared or distinct preferences (Morris 1988). In the case of shared preferences, competition for resources may occur. It is therefore possible to use habitat distribution patterns to evaluate the role of interspecific competition.

The necessary link between ecosystem knowledge and conservation

We have seen above how the loss of biodiversity is becoming an urgent issue that needs to be addressed by the conservation and scientific world before it becomes irreversible. Effective conservation measures are therefore required to guarantee the persistence of ecosystems that might provide invaluable services for human well-being (Braat & de Groot 2012), in most cases still undiscovered (Wilson 1992).

However, successful conservation management cannot be implemented without well-developed knowledge on species biology and processes occurring among species sharing the same habitat and, eventually, the same preferences.

The discipline of conservation biology has already contributed to mitigating anthropogenic actions on biodiversity at different organization levels and it has helped to reveal underlying mechanisms inducing variation in populations' demographic parameters (Primack & Miller-Rushing 2012). Thanks to this information, policy makers were able to act, most of the time under high urgency, setting up appropriate conservation programs to save endangered species from extinction.

Most of the conservation measurements put into place to preserve particular species deal only with the management of physical or habitat features without accounting for species interactions, which, most of the time, are unknown before the management action has been undertaken (Soulé et al. 2005). This kind of procedure is a risk for the ecosystem as ecological cascades may bring a better or a worst result than the expected one. For example, the eradication of invasive rats on North Island (Seychelles) in 2005 led to an unexpected decrease in the number of invertebrates, both on ground and leaves, despite the fact that rats were known to be feeding on invertebrates. This unexpected result was probably due to the trophic cascading effects of the removal of rats, which triggered a significant increase in land birds and lizards, and also in large invertebrates, all of which are feeding on small invertebrates and limited by rats (Galman 2011; Rocamora & Henriette, in press).

Therefore, when conservationists fail to understand the interactions occurring between species, conservation measurements might not achieve the desired results (Soulé et al. 2005). A solution to improve biodiversity maintenance can therefore be found in both practice and theory. Conservation evidence provide practical examples of what works in conservation (Sutherland et al. 2004a; Sutherland 2015) i.e. which actions have been already undertaken with successful results (see above). However, empirical studies on wild communities are strongly required to improve knowledge on mechanisms driving species coexistence (Morris 2003) and to track and predict changes on populations and communities when humans alter ecosystems properties.

In summary, theory and conservation should be closely related to effectively protect and manage important ecosystems and endangered or declining populations.

Seabirds: the balance of the ocean

The information required for conservation and management can be very difficult to obtain depending on the category of wildlife we want to study and on how complex is the surrounding habitat and ecosystem.

According to the BirdLife International/IUCN Red List assessment, the status of the world's birds has deteriorated over the past 20 years (BirdLife International, 2013). These changes were recorded in all major ecosystems but seabirds were found to be more threatened than other groups and declining the fastest (Butchart et al. 2004); therefore enough to be considered the most threatened group of birds (BirdLife International 2013; Croxall et al. 2012). In addition, seabirds are the most threatened marine taxonomic group in the world, with ~28% of species currently listed as threatened (IUCN 2012), plus others that are considered of special concern (Sydeman et al. 2012). The population decline of many seabirds needs attention within the world of conservation studies, in particular for the important role this group occupies in the marine ecosystem (Croxall et al. 2012). In fact, as top predators, seabirds are a valuable indicator of the marine ecosystem (Frederiksen et al. 2006; Furness and Camphuysen 1997; Zador et al. 2013). They can be used to evaluate the impact of climate change (Barbraud and Weimerskirch 2001; Barbraud et al. 2008) and fisheries (Catry et al. 2009a; Einoder 2009; Le Corre et al. 2012) and as indicators of prey stock (Le Corre and Jaquemet 2005; Lyday et al. 2015; Montevecchi, 1993; Piatt et al. 2007). It has been seen that seabirds' declines are often closely related to the worsening of the ecological conditions in marine ecosystems (Becker & Beissinger 2006; Bond & Lavers 2014). More knowledge in this field will allow to raise the understanding of basic processes linking seabirds with their environment, and to identify major threats and consequent actions oriented towards seabirds and marine ecosystem conservation.

As many seabird species home ranges are distributed widely across the world's oceans, seabird conservation issues need to be addressed globally (BirdLife International 2015). Within the seabirds, there is a category that requires particular attention, which is the order of the Procellariiformes (del Hoyo et al. 1992). Actually, 45% of species belonging to this order is threatened and information on population estimates, trends, movements at sea and population dynamic is lacking for many species. Moreover, Procellariiformes have to face a high number of threats both in land and at sea (Cooper & Baker 2008).

To improve the conservation efforts towards this category, the agreement on the conservation of albatrosses and petrels (ACAP) was constituted in 2004 (www.acap.aq). Since then, many actions have been undertaken, in particular towards the most threatened southern albatrosses, tackling especially birds by-catch in long-line fishery and introduced predators at colony levels (see for example Wanless & Maree 2014 and ACAP). If many procellariiformes species, like albatrosses and southern petrels, have been deeply studied over the last decades, others have been neglected. Information is mostly lacking for the burrow-nesting petrels (Cooper et al. 2006).

It is indeed very difficult to study burrow-nesting petrels because of their behaviour both in the colony and at sea (Warham 1996; Scott et al. 2009). The breeding sites are often inaccessible (remote islands, steep slopes, mountain tops) and in the case of nocturnal species, fieldwork must preferentially be conducted at night when most of the birds are present. As they nest in deep burrows, occupancy cannot always be assessed (i.e. it is difficult to conduct census work) and capturing individuals can also be a difficult task to achieve (i.e. difficulties in deploying and retrieving devices) (Buxton et al. 2015). As for the other categories of seabirds, it is difficult to identify optimal foraging areas as

they can depend on different environmental features that can vary in time, space and among species (Sekercioglu 2006). Luckily, with modern technology and with telemetry development, it is now relatively easy to track seabirds and identify the most exploited areas at sea (Le Corre et al. 2012). However, it is more difficult to determine if such areas are stable in time or if they move under the influence of preys-predators interactions and shifts (Corre 2001; Barrett et al. 2012)(i. e. pelagic fish predators-prey interactions) and changes in the marine ecosystems (Durant et al. 2009; Sydeman et al. 2012; Bond & Lavers 2014). Identifying seabirds' important areas at sea is therefore an essential (Lascelles et al. 2012) but challenging task as suitable areas can change in space and time.

Birds of the tropics

Even if it is hard work, knowledge on seabirds and on nest-burrowing petrels has exponentially grown over the last decades (see a review in Rayner et al. 2007). This was mainly due to: the availability of long term datasets, the development of statistical methods and tools for spatial and population analysis, the development of telemetry and related analysing tools, and the availability of more accurate remote sensing data (Wilson et al. 2002; Wakefield et al. 2009). Despite the increment and improvement on seabirds and marine ecosystem research over the past 30 years, most of these studies are focused on high latitude species and ecosystems dominated by high productivity with cyclic and abundant resources. In fact, even if increasing, the number of studies and publications on tropical areas are still insufficient when compared to quantity of research on temperate and polar regions. In tropical areas, resources at sea are more constant through the seasons but scarcer, less predictable and patchier than in temperate and polar waters (Weimerskirch 2007). Moreover, most of the tropical seabird species are associated and rely on schools of marine fish predators like tuna to make little fish more accessible on the surface (Le Corre and Jaquement 2005, Thiers et al. 2014). These factors can make uneasy the prediction and identification of important foraging areas for tropical seabirds. A special effort is therefore still required to increase the knowledge of seabirds breeding and foraging at tropical latitudes, and to understand the processes taking place between them and the environment they live in.

General questions and objectives for conservation

We've seen above how conservation science should adjust the methods to deal with biodiversity loss taking into account a more pressing and expanding anthropic development (Reyers 2004). Preserving nature and endangered or declining species is indeed becoming a process that cannot only be focused on nature reserves but should act at different levels of space (inside and outside nature reserves). It should also involve local communities and provide proper education to the new generations (Berkes 2007). However, as it often happens, financial resources are limited and in many cases the sole action of running and managing nature reserves is financially challenging. In fact, especially in developing countries, funding and local support to the preservation of species are often lacking, therefore the actions to undertake in support of biodiversity have to be well pondered and ranked in priority and feasibility. In such an environment, where priorities need to be taken into account, we first have to better understand the populations' status and the associated level of concern. The priority should be given to endemic endangered species and to key ecosystem species for which information is

lacking (Wilson et al. 2006). In many countries, the most valuable biodiversity is confined in nature reserves, often considered “island refuges” for many species (Kingsland 2002). Therefore, nature reserves offer a unique opportunity to better understand what is happening to species at a more general scale, although they can be considered a particular case study (Pullin 2010). As we explained above, nature reserves often host an incredible variety of different species that can survive thanks to the “facilities” that a protected area offers (i. e. control/absence of invasive predators and limited anthropic disturbance). These species often co-exist with unnaturally high densities caused by the lack of other suitable habitats outside the reserves. This can provoke an increment of interaction among species and high levels of competition among species for which ecological niches strongly overlap. Knowledge on species distribution and abundance, trends, habitat selection, movement, behaviour and foraging ecology is therefore essential to understand what is happening at community level and which are the mechanisms driving the community structure (Weiher et al. 2011). Once the mechanisms occurring among species and individuals within a community are clearer, actions can be informed and undertaken towards the species that need more help. For example, species that are declining or endangered and which are at the same time considered key species for a whole ecosystem. Action in nature reserves (and if possible outside) should be undertaken to avoid the loss of biodiversity. Acting in nature reserves is the easiest (and most of the time the main or even the only) path to undertake strict protection measures for species that depend on delicate ecosystem balances well beyond the boundaries of the reserves. If more resources become available, it then becomes possible to undertake further actions also outside nature reserves.

Conducting research, monitoring and conservation work in protected areas has also allowed scientists to acquire long term data that can be used to analyse the temporal development of communities and to establish how they react to the modification of resources. Long term monitoring protocols should therefore be implemented to better understand how populations change in a fast changing world.

Thesis outline and objectives

In small nature reserves, the conservation debate is often associated to practical issues, in particular the debate on whether or not to take action. Some conservationists defend the idea that once an island returns to its natural vegetation state after anthropogenic disturbance, nature should then follow its course and nothing should be managed. Others believe that what was once “natural” is long gone since humans started to interfere with original ecosystems, and also that nature reserves are now the only refuges left for many species. Therefore, if actions are required to help species, and in particular those that have the more unfavourable conservation status, they should be undertaken (Wynne 1998; Green et al. 2005). In little islands, the choice is even more difficult as often the species to preserve are many and crowded on a small patch of land. This is especially the case where management actions have to be well informed, as the consequences will involve many species. The outcome of interspecific interactions may change due to habitat modification; competition can intensify due to resource shortage and the management of a species is then directly related to the increment or to the decline of another (White 1978).

Considering that conservation management choices are difficult to make, the understanding of basic mechanisms acting between species and habitat, and among

species, is fundamental to inform conservation management. It is important to know what is happening in a population to decide on which best management actions need to be undertaken and with which order of priority (Sutherland 1998; Sutherland et al. 2004b; Fryxell et al. 2014).

With this research we analysed almost the full life cycle of two shearwater species breeding in a small nature reserve island in the Seychelles archipelago. We focus in particular on determining the ecological niche they occupy, both in land and at sea, and on possible competitive interactions that might occur between them. The use of a 2-competing species approach is important to highlight conservation trade-offs. Moreover, the fact that we approach it in almost the full life cycle, make our study particularly novel in the conservation framework.

To achieve the aforementioned general objective in CHAPTER 2 and 3 we investigate habitat selection and assess abundance, distribution and trends of two species of shearwaters breeding in Seychelles. At the same time, given the difficulty of census taking for nest-burrowing seabirds, we propose methods that could be also applied to other species. Furthermore, we investigate their life at sea during both breeding and interbreeding periods in order to identify the marine features selected during the birds' dispersion (CHAPTER 4 and 5). Based on selected habitat and oceanographic features, habitat suitability maps were created per each breeding period in order to identify the areas in the Indian Ocean which are more important for the two species (CHAPTER 4). In APPENDIX I we include the data on the breeding success and nest occupancy collected during the research.

In this study, nearly all aspects of the life cycle are investigated except the stage from fledging to breeding adult (Figure 1.1). The CHAPTERS 2 and 3 describe the life in-land while the CHAPTERS 4 and 5 describe their life at sea. Given all this information, possible competition between the two species can be assessed and management actions towards their conservation informed.

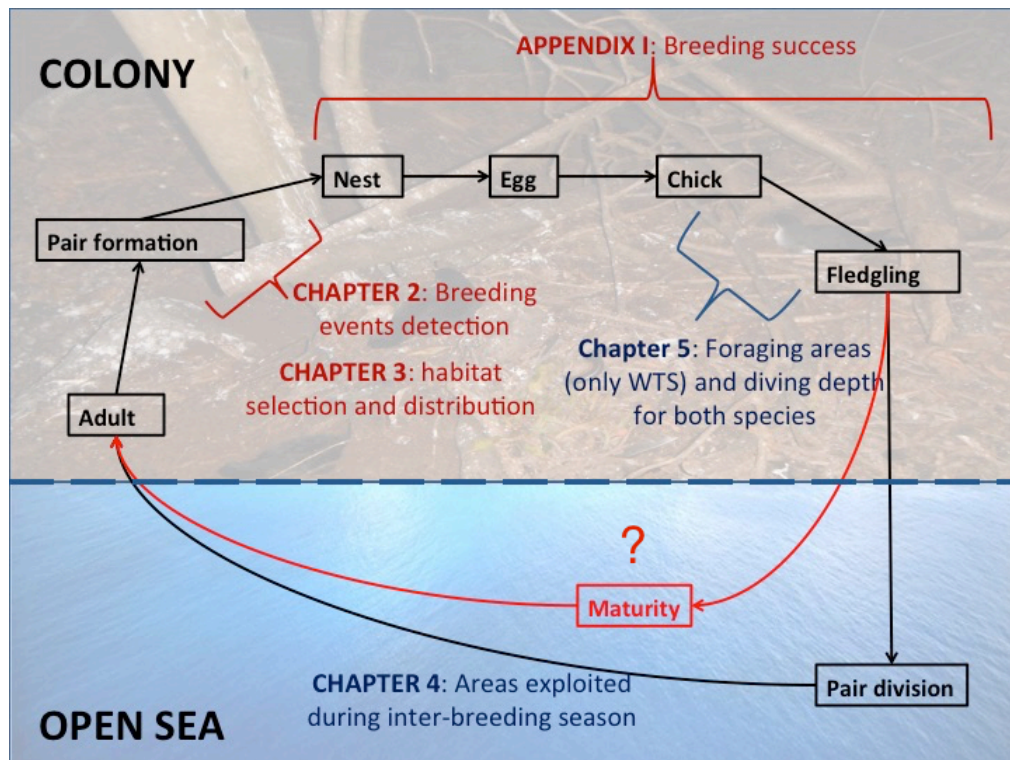


Figure 6.1. Thesis scheme.

1.2 General Methods

Study site

Our study was carried out in the Seychelles archipelago, which is located between c.04°S to 10°S and 46°E to 54°E, in the western Indian Ocean. In 1968 these islands were already considered as a sanctuary for biodiversity and an important place to preserve when, in the first issue of the journal “Biological conservation” Stoddard and Polunin underlined the importance of the archipelago for both birds and vegetation (Polunin 1968; Stoddard 1968). These islands do not only host rarities and endemic species, but also some of the largest seabird colonies of the tropical Indian Ocean (Stoddard 1984; Skerrett et al. 2001). They are part of one of the most important hotspots for biodiversity in the world (Madagascar & Indian Ocean Islands), to which both attention and priority in terms of conservation should be given (Myers et al. 2000; Critical Ecosystem Partnership Fund 2014).

The archipelago has a total landmass of 455 km² spread across an Exclusive Economic Zone of about 1,374,000 km² (Rocamora & Skerrett 2001). It consists of 155 islands divided into two groups: the granitic islands, which form the inner islands (together with the two northern coralline islands of Denis and Bird) and 4 groups of coralline islands, called outer islands. The inner islands lie on the submerged Seychelles Bank and are the world’s only oceanic islands of continental rock. They have been isolated from any other land mass for 65 million years, before mammals evolved; hence there are no naturally occurring non-flying mammals (Skerrett et al. 2001). Such isolation has led to a high number of endemic species of both fauna and flora.

The 4 groups of outer islands are located west and southwest of Seychelles. They count a total of 115 main islands excluding the smallest islets and they host many numerous colonies of seabirds; the endemism (birds, plants, reptiles, invertebrates) are restricted to the southernmost of the 4 archipelagos, the Aldabra group (Rocamora & Skerrett 2001).

The climate of Seychelles is tropical and it is influenced by two seasonal wind systems: monsoonal wind shifts and the South Indian Ocean subtropical anticyclone. The South-east monsoon is relatively dry and blows from May until October. It is characterized by strong and unidirectional wind coming from the Southeast. The temperatures average 25°–30°C at sea level and humidity is around 80%. The Northwest monsoon blows from October to April. The wind is more changing than unidirectional and the temperature is slightly higher (up to 35°C) as are the humidity and the rainfall.

Rainfall is higher in the high granitic islands than in the flat coralline ones, due to the influence of relief. The annual mean rainfall in the inner islands is approximately of 2,400 mm; while in the outer islands it varies from 1,000 mm to 1,500 mm (Rocamora & Skerrett 2001).

The Republic of Seychelles counts about 89,000 inhabitants and its population is incrementing (World Bank 2013, www.worldbank.org). Nearly the entire population of Seychelles (99.7%) lives in the granitic group, with 90% located on the main island of Mahé (15,500 ha) and most of the rest on Praslin (2,756 ha) and La Digue (1,101 ha).

The first human settlement was in 1770, when the French colonized the islands. The islands then came under British rule in 1815 and the independence of Seychelles was obtained in 1976.

Colonization of the islands by humans resulted in a huge ecological trauma to the fragile ecosystems. The human colonization brought intense habitat destruction (e.g. forest

clearance, wetland drainage), the introduction of alien, invasive plants and predators (e.g. rats, cats) and unsustainable exploitation of the fauna. Much of the original vegetation was cleared throughout Seychelles for timber production or agriculture, particularly coconut plantations (for copra) and cinnamon exploitation in the inner islands. These industries used to be the major source of income together with agriculture and traditional fishing until the 1970s. They have been replaced recently by tourism since the opening of Seychelles International Airport on Mahé in 1972, while the industrial fishing industry (mainly tuna fishing and canning industry) became the second largest source of income (Critical Ecosystem Partnership Fund 2014). For example, in 2010, c. 60 metric tons of tuna were caught in the Seychelles Economic Exclusive Zone (Seychelles Fishing Authority, 2014) representing 1.4 % of the world tuna catch based on the FAO reports (<http://www.fao.org/fishery/statistics/tuna-catches/query/en>). In addition, offshore waters are now dedicated to oil exploration as indicated in the 2013 model petroleum agreement (www.petroseychelles.com).

Only a few species are known to have become globally extinct in the Seychelles, mainly birds (Skerrett et al. 2001; Critical Ecosystem Partnership Fund 2014), which is much less than in the Mascarene islands (Cheke & Hume 2008). However, it is likely that more species of plants and animals may have disappeared even before they could be described (see for example Cheke & Rocamora, 2013). The Seychelles are characterized by high levels of biodiversity overlaid with high human and economic pressure, particularly since the 1970s. Since then, many nature reserves and marine parks were established with the aim of protecting the survivor species, and the Seychelles have now over 50% of its land territory under legal protection status (Critical Ecosystem Partnership Fund 2014).

The Seychelles also hosts 20 terrestrial Important Birds Areas (IBA) of which 12 have been classified predominantly for their seabird colonies or congregations (Rocamora & Skerrett, 2001). One of the most important IBAs of Seychelles is Aride Island Nature Reserve, the study site for our research. Aride (4° 12' 46"S; 55° 39' 53") is the northernmost of the granitic islands, it has a surface of 73 ha (69 ha in horizontal projection) of which c. 5 are flat (plateau) and it has a maximum height of 135 m asl.

Aride first appears on charts drawn up by Du Roslan aboard the *Heure du Berger* between December 1770 and February 1771. By 1868, when the naturalist Perceval Wright visited, the plateau was cleared for crops. Coconuts were planted in the 1920s and 1930s, since then the plateau was covered in a thick coconut plantation while the rest of the vegetation on the hill was continuously cleared to facilitate sooty terns (*Onychoprion fuscatus*) breeding for egg harvesting. At this time, the island hosted about 20 people working for the plantation. Pigs, chickens, goats and cats were also present, creating major disturbance to the local fauna (Warman & Todd, 1984). Fortunately *Rattus sp.* never colonized the island and the only introduced mammal that has not yet been eradicated is the house mouse (*Mus domesticus*), an alien species that does not seem to have had a major impact on the ecosystem (Rocamora & Henriette, in press).

In 1973, Aride was purchased by the Royal Society for Nature Conservation (RSNC) with funds donated by Christopher Cadbury and received legal protection as a Special Reserve under Seychelles law in 1979. Once it became a nature reserve, an intensive project of habitat restoration started and the coconut plantation together with the other non-native species (except for the mice) were removed (Warman & Todd 1984). After the removal of the plantation and the end of the vegetation clearance on the hill, the native vegetation recolonized the island, including the fast growing *Pisonia grandis* that expanded quickly across the whole island and is now the dominant tree species. The

mixed native woodland includes also *Ficus lutea* and *F. reflexa*. The native fern species *Nephrolepis biserrata* has also expanded under the canopy cover, reaching 1.5 m height in thick patches (Senterre et al. 2010). Granite outcrops and relictual glades are still present on the hill, where there are also small areas of *Euphorbia pyrifolia* scrub. The plateau is also covered by woodland replanted with native species (*Callophyllum inophyllum*, *Terminalia catappa*, *Morinda citrifolia*, etc.) and a small wetland, where the rare black-mud terrapin (*Pelusios subniger parietalis*) was reintroduced in 2012, is also present. Five Seychelles endemic landbirds occur on Aride, three of which are globally threatened species and were reintroduced in 1988 (Seychelles warbler *Acrocephalus sechellensis*) and in 2002 (Seychelles magpie-robin *Copsychus sechellarum* and Seychelles fody *Foudia sechellarum*).

Since 1973, the only human inhabitants of Aride are the reserve's staff members and volunteers, with a maximum of 7- 10 people.

At present, the island hosts the largest and most important seabird populations of the Seychelles granitic archipelago about one million breeding seabirds of 10 species (Rocamora & Skerrett, 2001). These include the world's largest colony of lesser noddy (*Anous tenuirostris*) and the only surviving roseate tern (*Sterna dougallii*) colony in the granitic islands. Aride is also the only nesting site north of the Aldabra group of the red tailed tropicbird (*Phaethon rubicauda*), which is still found in low numbers (2-3 pairs). The sooty tern still breeds in high numbers under the canopy cover which now covers much of the island (the only known case in the world, Chris Feare, pers. comm); this is probably the last viable colony in the granitic islands and the only one protected from egg harvesting (still legal in the Seychelles) although poaching of eggs does occur on Aride. Other seabirds breeding on Aride include the fairy tern (*Gygis alba*) and the brown noddy (*Anous stolidus*), both represented by the largest colonies in the Seychelles. The bridled tern (*Sterna anaethetus*) also breeds in low numbers. Aride hosts also a mixed colony of shearwaters, the tropical shearwater (*Puffinus bailloni*) and the wedge-tailed shearwater (*P. pacificus*). The tropical shearwater population is the probably largest known in the world (del Hoyo 2014, Safford and Hawkins, 2013) while the wedge-tailed shearwater one is the second largest in the Seychelles archipelago (after St Joseph; Kappes et al. 2013). Seabird numbers are largest during the Southeast monsoon, from May to October, as this is the main breeding season for many species. However, the white-tailed tropicbird (*Phaethon lepturus*), the fairy tern, the tropical shearwater and the bridled tern nest all year-round.

Aride Island appears clearly as a key seabird conservation hot spot within the Western Indian Ocean basin, especially being surrounded by economical activities related to the marine environment. It is therefore an optimal study site to understand trends and mechanisms involving the whole Western Indian Ocean seabirds' community. Seabird monitoring on Aride has been conducted regularly since it became a nature reserve using standardized methodologies (Sampson & Rocamora 2008). Aride has its own environmental management plan that is updated every 5 to 10 years (Sampson 2006).

Study species

The decision to study the two species of shearwaters breeding on Aride Island was taken for many reasons.

First of all, these two populations have been monitored since 1979. Even if the previous censuses have been of irregular quality, particularly with regards to the number of the sampling areas monitored and their insufficient representativeness, this

is one of the very few cases in the tropical world where two populations of shearwaters have been monitored for so long with the opportunity of providing some likely trend (taking into account the above limitations).

Second, even if previous surveys are available, they were indeed limited in terms of accuracy and precision; therefore there was a need for an exhaustive census that could provide a reliable estimate of the current number of breeding pairs. This is particularly important for the tropical shearwater as *Aride* is suspected to be the largest colony in the world, and data on this species are lacking worldwide (Safford & Hawkins 2013).

Third, these are the only two tropical shearwaters species breeding in the Western Indian Ocean, so they can be considered representative for this region. For example, the tropical shearwater has sibling subspecies in the Indian Ocean basin, sharing probably the same ecological niche (see below). Very little or no information is available on these other populations, some of which are probably threatened (Safford & Hawkins 2013; Shirihai & Bretagnolle 2015). Therefore more general information on the Tropical shearwater foraging areas and on its behaviour at sea and in land can help to gain a better understanding on the biology and status of taxa belonging to the same species complex.

Forth, it is rare to find two species of shearwater sharing the same colony space. In La Réunion Island, for example, both species breed in the same island but they are segregated over an altitudinal gradient (Bretagnolle 2000). Therefore, at the *Aride* colony, it is possible to investigate if competition mechanisms exist between the two species and if one species may eventually over-compete the other. The wedge-tailed shearwater is known to be a very aggressive competitor for breeding sites if sharing mixed colonies with other nest-burrowing seabirds (Villard et al. 2006), but to our knowledge it has never been studied in mixed colonies with another shearwater species.

Fifth, these two species (like the other 8 seabirds species breeding on *Aride*) breed in a secondary forest that has grown naturally after severe anthropogenic habitat modifications. Investigating their habitat selection, distribution and the observed trends can improve the understanding about the processes involved between a fast changing habitat and the species living in it.

Finally, both species used to be harvested for food and, even if protected, they are still poached. A better understanding on their distribution and trends can possibly assess the effect of this practice on the population.

Species description and distribution

The Tropical shearwater is one of the smallest species in the *Puffinus* genus (c.200 g; Brooke, 2004). Its range includes the tropical Indian and Pacific Oceans where different subspecies occur (del Hoyo et al., 2012). In the western Indian Ocean, it is found on La Réunion Island (subspecies *bailloni*) and on the Seychelles archipelago (subspecies *nicolae*) with small colonies also on Comoros and Maldives (Bretagnolle et al. 2000; Shirihai & Bretagnolle, 2015). Its breeding biology, foraging behaviour and ecology are still poorly known (del Hoyo et al. 2012; Skerrett et al. 2001). Most colonies have been severely impacted by rats, which led to extinctions on several of the Seychelles islands although small numbers still breed sporadically on some rat infested islands including Mahé (at c. 600 asl) and Marianne Islands (G. Rocamora 2012, pers. obs.) and in the Amirantes D'Arros and St Joseph (since 2014; Rainer von Brandis, pers. comm.) and Desroches (since 2015; G. Rocamora, P. Nogués & J. Russell, unpublished). Yet, the

species has recently been assessed as of Least Concern under the IUCN Red List Category (BirdLife International, 2014). Estimating tropical shearwater population size is notoriously difficult, and indeed no accurate world estimates, nor trends, are available.

The wedge-tailed shearwater is twice as large (c. 400 g) and monotypic, with a breeding range extending throughout the tropical and subtropical latitudes of the Pacific Ocean, including the east coasts of Australia, New Caledonia and Polynesia, and the Indian Ocean (Brooke 2004; del Hoyo et al. 2012b; Harrison, 1983). It has been well documented in different breeding sites for which population estimates and trends are available (Burger and Lawrence 2001; Dyer 2003; Dyer et al. 2005; Kappes et al. 2013). It is classified as Least Concern (BirdLife International 2012) even though population trends in several localities are negative, threatened by unsustainable levels of fisheries exploitation, persecution and predation by invasive species (Brooke 2004; Dyer 2003; BirdLife International 2012). In the granitic islands, the main colonies are located on Cousine (considered the largest colony), Aride and Cousin (Rocamora & Skerrett, 2001). The largest colony of the outer islands is on St Joseph atoll, in the Amirantes (Kappes et al. 2013). Smaller colonies are found on Ile aux récifs, Mamelles and other smaller granitic islets, and also on other coralline islands, such as Bird Island, D'Arros, Desnoeufs, Marie-Louise (Skerrett et al. 2001). Small colonies are also known on Denis Island, North Island, Conception, Petite Soeur, Alphonse, Desroches and Ste Anne; these have appeared or have increased significantly following the eradication or the control of rats and cats (Rocamora & Henriette, in press).

The two studied species share the same breeding habitat, but strongly differ in their size, hence in their ability to compete for burrows, and in their breeding phenology. The tropical shearwater breeds all year round while the Wedge-tailed shearwater breeds synchronously between September and March. Population size estimates for both species are available for Aride Island since 1979 (Table 3.3), but until 1998 the survey methods were only based on burrow counts without accounting for burrows occupancy. Afterwards, even if an implemented protocol accounting for burrow occupancy was put in place in 1997 (Betts 1998), the surveyed area (0.27 % of the island) was not large enough to provide a reliable population size. In addition, data analysis did not account for the simultaneous presence of the two species and for habitat selection.

CHAPTER 2

Analysis of playback census to estimate the density of cavity-dwelling birds

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Manuscript accepted for publication: Bonnet-Lebrun A. S., Calabrese L., Rocamora G., López-Sepulcre, A. (accepted). Analysis of playback census to estimate the density of cavity-dwelling birds. Journal of Avian Biology.

Abstract

1. The conservation of elusive species relies on our ability to obtain unbiased estimates of their abundance trends. Many species live or breed in cavities, making it easy to define the search units (the cavity) yet hard to ascertain their occupancy. One such example is that of colonial seabirds like petrels and shearwaters, which occupy burrows at night to breed. In order to increase the chances of detection for these types of species, their census can be done using two independent methods to check for cavity occupancy: visual inspection, and acoustic response to a playback call.
2. This double-detection process allows us to estimate the probability of burrow occupancy by accounting for the probability of detection associated to each method. Here we provide a statistical framework to estimate the occupancy and population density of burrow-dwelling species. We show how to implement the method using both Maximum Likelihood and Bayesian approaches, and test its precision and bias using simulated datasets. We subsequently illustrate how to extend the method to situations where two different species may occupy the burrows, and apply it to a dataset on Wedge-tailed Shearwaters *Puffinus pacificus* and Tropical Shearwaters *P. bailloni* on Aride Island, Seychelles.
3. The simulations showed that the single-species model performed well in terms of error and bias except when detection probabilities and occupancies were very low. The two-species model applied to shearwaters showed that detection probabilities were highly heterogeneous. The population sizes of Wedge-tailed and Tropical shearwaters were estimated at 13,716 and 25,550 pairs respectively.
4. The advantages of formulating the playback-call census method statistically is that it provides a framework to calculate uncertainty in the estimates and model assumptions. This method is applicable to a variety of cavity-dwelling species where two methods can be used to detect cavity occupancy.

2.1 Introduction

Estimating abundance is central to most ecological studies. In the context of conservation, abundance estimates provide baseline information about the status of a population (Sutherland et al. 2004; Bibby et al. 2012). They allow the tracking of temporal changes and the study of habitat preferences, and help assess the impact of environmental and land use changes (Gregory et al. 2004). To meet this need, a plethora of field and statistical methods have been devised to improve abundance estimates, adapted to the habits of a variety of species. Central to this exercise is accounting for the widespread problem of imperfect detection (Borchers et al. 2002; Royle et al. 2005; Scott et al. 2009).

For the vast majority of populations, be it due to logistical constraints or species elusiveness, it is impossible to directly count all the individuals present at a given time. Unbiased estimates of population abundance therefore require estimating the probability of detection of individuals present in the population (MacKenzie et al. 2005). This can be estimated from a variety of sampling designs like double observer counts (Forcey et al. 2006), distance sampling (Buckland et al. 2001), or capture-mark-recapture (McCrea and Morgan 2014). Modern statistical methods can use these designs to jointly estimate species detection probabilities and abundance, thus accounting for the uncertainty of both estimates. Despite this, it is not uncommon for practitioners to independently estimate the detection probability using a subset of data, and later apply it as a correction factor to individual counts (e.g. Azuma et al. 1990; Zielinski and Stauffer 1996; Bodkin and Udevitz 1999; Burger and Lawrence 2001; Thompson 2002; Kissling et al. 2006). This *ad hoc* application of correction factors, however, makes it difficult to produce abundance confidence intervals that account for the uncertainty in the detection factor estimation. In the worst cases, ignoring uncertainty in correction factors can lead to grossly misleading conclusions, such as was illustrated in a recent re-analysis of tiger recovery (Gopalaswamy et al. 2015).

In species that inhabit dens or burrows, estimates of population densities rely on our ability to infer the proportion of those cavities that is inhabited by a breeding pair. This is the case of burrow nesting seabirds, which has a tradition of correcting for detectability through *ad hoc* application of correction factors (Warham 1996; Ratcliffe et al. 1998; Burger and Lawrence 2001; Scott et al. 2009). For example, some studies have used multiple visits to ascertain occupancy in a subsample of burrows, calculated an average occupancy rate and applied it to the total number of burrows of the sample area (Rayner et al. 2007; Whitehead et al. 2014). Other studies use the playback method, which combines visual and acoustic detection, and calculate a playback response rate which, applied to the number of burrows with undetected birds in it, gives an estimate of the proportion apparently empty burrows that contained an unresponsive bird (James and Robertson 1985; Burger and Lawrence 2001). While some studies use both methods only on a subset of data to later apply the calculated playback response rate to surveys using only acoustic sampling (e.g. James and Robertson 1985), others use both detection methods for all burrows (Burger and Lawrence 2001). In the first case, the number of occupied burrows is calculated as:

$$\hat{N} = n_R p_R, \quad (\text{eqn 1})$$

where n_r is the number of burrows that responded to the playback call, and p_r is the response rate calculated from the subsample as the proportion of visible birds that responded to the playback (James and Robertson 1985). When both methods are used for all burrows, the total number of occupied burrows N is subsequently estimated using the following formula:

$$\hat{N} = n_V + n_0 \frac{n_{R0}}{n_{VR}} \quad (\text{eqn 2})$$

where n_V is the total number of birds seen, n_0 is the number of burrows with undetected birds (not seen nor heard), n_{R0} is the number of birds that responded but were not seen, and n_{VR} is the number of birds that were seen and responded.

While the above methods address the bias in our estimates of burrow occupancy by accounting for imperfect detection, they do not provide measures of uncertainty in the estimate. Because uncertainty in population estimates is key to the management of species, it is clearly desirable to formalize the joint estimation of detection and abundance probabilities in a formal statistical framework.

The aim of this article is to provide a statistical framework for the analysis of playback census. First, we derive the necessary likelihood functions. Second, we will implement them on simulated data using both maximum likelihood and Bayesian approaches, in order to assess the bias and precision of the occupancy estimates. Third, we extend the approach to cases where a burrow can be occupied by two different species. Finally, we implement the approach using data on two species of burrow-nesting seabirds, the Wedge-tailed *Puffinus pacificus* and the Tropical shearwater *P. bailloni*, breeding on Aride Island, an Important Bird Area of Seychelles (Skerrett et al. 2001). Although particularly useful for the census of burrow-nesting seabirds, the approach is applicable to any species where two independent methods of detection (e.g. passive sighting and active luring) can be applied to estimate the occupancy of an animal's dwelling (e.g. crabs in burrows, fish in shelters, or woodpeckers in tree-holes).

2.2 Materials and Methods

STATISTICAL FRAMEWORK

Consider a set of m burrows that may be occupied by the species of interest. For each burrow, the detection procedure occurs by two independent methods with different detection probabilities: visual examination and playback. The data is arranged in a matrix X of m rows and two columns, whereby for each burrow i , elements $x_{i,1}$ and $x_{i,2}$ contain a 0 or 1 depending on whether an individual was detected or not with either the first (visual) or second (playback) method respectively. For example, an individual (or pair) that was not seen but heard on burrow i , will correspond to $x_i = \{0,1\}$. If we denote the probability of occupancy of the burrow ψ , the probability of visual detection p_s , and the probability of playback response p_r , the likelihood of all four possible outcomes is given in Table 2.1. The total likelihood of the data X is therefore:

$$L(X | \psi, p_s, p_r) = \prod_{i=1}^m \{ \psi [p_s x_{i,1} + (1 - p_s)(1 - x_{i,1})] [p_r x_{i,2} + (1 - p_r)(1 - x_{i,2})] + (1 - \psi)(1 - x_{i,1}x_{i,2}) \}$$

(eqn 3)

Note that for this to be true, we must make the following biological assumptions. First, we assume that each burrow can only be occupied by a single individual (or pair). Second, we assume independence of the two detection methods: in other words, visual inspection does not affect the probability of response nor vice-versa. In order to ensure this is fulfilled, it is recommendable to use the potentially more disturbing method last (e.g. playback should be done after visual inspection, to ensure birds did not change their behaviour in ways that affect their visibility). Third, it assumes that unoccupied burrows represent the absence of a breeding bird, rather than a temporary absence (e.g. to forage). To ensure this, it is important to time the census during the animal's inactive period of the day (e.g. night for most burrow-nesting seabirds). The latter assumption can be relaxed by the use of repeated observations through time.

The estimation of parameters ψ , p_s , and p_r , can proceed by Maximum Likelihood or Bayesian methods. For the latter, it will be necessary to define priors. Since all three parameters are probabilities we will use a uniform distribution bounded between 0 and 1 as recommended in (Royle and Dorazio 2008). The total number of individuals in a plot can be estimated as $\hat{N} = \psi m$.

SIMULATED DATASETS AND PERFORMANCE COMPARISON

In order to evaluate the performance of both Maximum Likelihood and Bayesian methods, we simulated a series of datasets. All datasets represented a plot with 30 burrows (representative of the number of burrows found in a typical plot for the shearwater case study exposed below). Data was generated using binomial trials for three-way combinations of the following parameter values. For both detection probabilities p_s and p_r , we used $\{0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9\}$. The occupancy probabilities ψ used were $\{0.1, 0.3, 0.5, 0.7, 0.9\}$. For each combination, we performed a total of 20 simulations.

Maximum Likelihood estimation was performed in program R, using function `mle2` in package `bbmle` (Bolker and R Development Core Team 2014). Bayesian estimation was

implemented in JAGS. As uninformative priors for all parameters (p_{oc} , p_v , p_r) we used a uniform distribution from 0 to 1. For each estimation we ran 2000 chains with a burnin of 500.

We evaluated the performance of the estimation by calculating the average error and bias in estimating the total number of occupied burrows, the most likely measure of interest. As a measure of error we used the root mean squared error (RMSE):

$$RMSE = \sqrt{\frac{(\hat{N}-N)^2}{n}}, \quad (\text{eqn 4})$$

where N is the known population size, \hat{N} is its estimate, and n is the expected number of occupied burrows (number of burrows $\times p_{oc}$). The results are presented in standardized units by subtracting the mean RMSE for a given parameter combination and dividing by its standard deviation (Figure 2.1).

We calculated relative bias as the proportional difference between estimated and known population size $\frac{(\hat{N}-N)}{N}$ (Figure 2.2).

EXTENSION TO TWO SPECIES

It is not uncommon for burrows and other types of refuge to be suitable to more than one species. In the example of a two-species scenario where the burrow can be occupied by either species A or B alternatively it is straightforward to extend the model. We do so by assuming species-specific occupancies (ψ_A , ψ_B) and detectabilities (p_{vA} , p_{vB} , p_{rA} , p_{rB}). If we assume that it is only possible to find an individual (or pair) of one or the other species (not both), we need to constrain the model so that $\psi_A + \psi_B \leq 1$. Table 2.2 specifies the likelihood for all possible data outcomes. Note that in this case, the way to code the data is similar to the one-species case, but with 1 or 2 representing detection of species A or B respectively. For example, if species B is seen but not heard in burrow i , $x_i = \{2, 0\}$. The total data likelihood is again the product of likelihoods for all burrows.

CASE STUDY: ESTIMATING SHEARWATER DENSITIES ON ARIDE ISLAND

We here present the application of the two-species model to the estimation of a mixed colony on Aride Island (Seychelles) with two breeding shearwaters: the wedge-tailed *Puffinus pacificus* and tropical shearwater *P. bailloni*. Aride Island Nature Reserve comprises 73 ha and is suspected to harbor the largest colony of *Puffinus bailloni* in the world (Del Hoyo et al. 1992, Skerrett et al. 2001). Both species breed in the same type of natural burrow on the hillsides of the island. While *P. pacificus* is a seasonal breeder found mainly from September to February, *P. bailloni* has no clear breeding season in Seychelles, and incubating birds may be found all year round (Skerrett et al. 2001).

To carry out the census here analyzed, we followed the playback census protocol described in (Betts 1998). The census plots were sampled in November 2011, February 2012 and May 2012 (only once per plot), in order to ensure good representation of *P. bailloni*. For the seasonal *P. pacificus*, only the November and February months are considered. We surveyed 19 circular plots of 100 m² randomly selected in 1996 for a previous survey (Betts 1998). All surveys occurred at night between 20:00h and 23:00h once every census month. In each plot, we noted all potentially suitable burrows and inspected them visually for the presence of a nesting bird of either species. We played recorded male-female duet calls for both species (Rocamora et al. 2000) in the case of unknown content, and for the observed species when the bird was visible. We played the

call at the opening of the burrow and noted whether the bird responded by the end of the recordings (1:24 min for *P. bailloni* and, 1.58 for *P. pacificus*).

We used the two-species model specified above to estimate the average densities of shearwaters on the island. In order to account for plot-variation in occupancy and produce estimates of average island densities, we modelled species-specific occupancy probabilities ψ as a random effect. That is, rather than estimating plot-specific occupancy probabilities, given plot i and species S the probabilities of occurrence followed a logit-normal distribution:

$$\text{logit}(\psi_{S,i}) \sim N(\mu_{\psi S}, \sigma_{\psi S})$$

We evaluated the importance of heterogeneity in detection probabilities by comparing models that differed on whether the detection probabilities ($p_{VA}, p_{VB}, p_{VA}, p_{VB}$) were fixed or randomly (logit-normally) varying across plots. As a measure of model performance we used the Deviance Information Criterion, DIC (Spiegelhalter et al. 2002; Supplementary material Table ESM2.1).

Parameters were estimated using a Bayesian framework, as it performed better in the simulations. We specified the following uninformative parameter priors for the random variables:

$$\mu \sim N(0,10)$$

$$\sigma \sim \text{Unif}(0,10)$$

When probabilities were set as constant across plots, we used a uniform prior ranging from 0 to 1.

We ran three independent MCMC chains with 10 000 iterations each, a burnin of 5000 and thinning of every 10 samples. Convergence was considered achieved when the Gelman-Rubin statistic (Gelman and Rubin 1992) for all parameters was lower than 1.1.

2.3 Results

SIMULATED DATASETS AND PERFORMANCE COMPARISON

Figures 2.1 and 2.2 show the standardized RMSE and bias for the estimation of shearwater densities in the simulated plots. Models performed better when the probability of occupancy increased, both in terms of bias (Figure 2.1) and error (Figure 2.2). This is because higher occupancies imply larger sample sizes to estimate detection probabilities. Only plots with $\psi = 0.1$ (and therefore an average of 3 out of 30 occupied burrows) showed considerable levels of error and bias. Expectedly, the models also performed better when the probabilities of detection increased. Note that the two probabilities of detection are interchangeable. The Bayesian framework performed worse under low occupancy rates and very different detection probabilities among both methods (i.e. one being high and the other low).

CASE STUDY: ESTIMATING SHEARWATER DENSITIES ON ARIDE ISLAND

Table ESM2.1 (External Supplementary Material) shows the performance of two-species shearwater models varying in assumptions of detection heterogeneity. The model with heterogeneity in all probabilities of detection was clearly superior ($\Delta\text{DIC} = 24.08$). The parameter estimates for the best model are shown in Table ESM2.2 (External Supplementary Material) and Figure 2.3.

The total population sizes were estimated at 25,550 pairs (95% CI: 23,667 - 28,777) for *P. bailloni* and 13,716 pairs (12,909 - 15,874) for *P. pacificus*. This is considerably lower than previous estimates a correction factor approach (Sampson and Sampson 2007), particularly for the *P. bailloni* (estimated at 98,000 pairs in 2006-2007), but more research is needed increasing the number of plots and accounting for spatial heterogeneity in order to ascertain whether there has been a true decrease in the population.

2.4 Discussion

We have described a simple statistical framework to estimate the abundance of cavity-dwelling species. In these species, density estimation reduces to a problem of occupancy, where the key quantity to estimate is the probability of an individual (or breeding pair) being present in the cavity. This is analogous to the estimation of species occurrence in occupancy models (MacKenzie et al. 2005).

While species occupancy models typically use multiple site visits and a single detection method to estimate detection probabilities, some studies have extended them to incorporate multiple detection methods (e.g. Coggins et al. 2014). Nichols et al. (2008) provide a general framework for analysing multiple-method data on species occurrence. The method we presented is closely related to the special case of single site visits, yet applied to the estimation of abundance, rather than presence, when the species inhabits discrete units such as cavities. This is important when extending the models to multiple species. While species occurrence models should allow for multiple species to share a plot; each cavity cannot be shared by more than one individual or pair of a single species.

Our formulation bears some implicit assumptions to be considered when interpreting the density estimates. The first one is that all birds are present in their burrow at the time of the survey. If individuals are absent foraging at the time of sampling, or their breeding attempt has ended before sampling, they will not be accounted for. In the case of shearwaters, the first aspect is minimized by performing the census at night, when birds return to their burrows. This problem is also minimized during egg-laying, incubation, or brooding chick stage, when at least one bird (one of the adults or the chick) stays behind in the burrow at all times. If this issue, however, is deemed important for the species at hand, the design can be extended to performing multiple visits per burrow in an analogous way to Nichols et al. (2008). Other possible extensions to the method include modeling the dependence of occupancy or detection probabilities on habitat characteristics. This may be important to yield reliable predictions at larger scales that include a variety of environments.

Although we have illustrated an application to the study of shearwaters, the method we outline is applicable to any cavity-dwelling species that may be sampled non-invasively using two detection methods. This may include, not only a variety of burrow-nesting birds such as shearwaters, petrels, penguins or burrowing owls, for which the playback detection is commonly used (e.g. Haug and Didiuk 1993, Jouventin and Aubin 2002, Barbraud and Delord 2006, Conway et al. 2008); but also a variety of other animals like den-living mammals and burrowing crabs or spiders.

One advantage of our proposed method is that it does not require destructive sampling to yield reliable estimates of burrow occupancy. Destructive methods such as burrow excavation have been used to calibrate imperfect methods of detection (Lawton et al. 2006, Newman et al. 2009 for seabirds, Pombo and Turra 2013 for crabs). This brings ethical and conservation issues. Simultaneous use of two imperfect methods allows the estimation of occupancy without the need to ascertain it destructively.

Accurately representing the uncertainty in our estimates of species population densities is of central importance to effective and sustainable management (Ludwig et al. 1993). This is the main advantage of our proposed method over other methods used to estimate densities of cavity-dwelling species. While these methods aim to account for

detection bias through application of correction factors, they do not calculate the uncertainty caused by imperfect detection (e.g. James and Robertson 1985, Warham 1996, Ratcliffe et al. 1998, Gusset and Burgener 2005, Scott et al. 2009, Oppel et al. 2014). Moreover, they do not account for possible spatial heterogeneity in the probabilities of detection. For example, Conway et al. (2008) showed that the detection of burrowing owl (visual and playback response) depends on factors such as ambient temperature. In our application, the best models for both species incorporated variation in both visual and acoustic detection probabilities. The problem of census correction and calibration factors extends beyond studies of burrow occupancy. Gopalaswamy et al. (2015) showed that using *ad hoc* calibration indexes relating track-counts to camera-trap-based population estimates resulted in a deceiving overestimation of Indian tiger recovery. This highlights the importance of jointly estimating observation and occurrence in our census of animal populations.

2.5 Acknowledgments

We would like to thank the staff and volunteers of Aride Island for assistance in data collection, and Vincent Bretagnolle and Swanne Gordon for comments and discussion. ALS would like to thank M. Betts for an inspiring introduction to play-callback census. This research was approved by the Seychelles Bureau of Standards (Research Permit N°A0157). Funding was provided by the Island Conservation Society, the CNRS, Fondation TOTAL (to LC and GR), the École Normale Supérieure de Paris (to ASBL) the Agence Nationale de la Recherche's project EvoRange (to ALS), and the Direcció General de la Recerca de Catalunya (2009-SGR-481, to ALS).

Tables

Table 2.1. Likelihood of each possible data scenario in a single species case

Scenario		Data	Likelihood
Sighting	Response	$x_{i.}$	$L(x_{i.} \psi, p_V, p_R)$
Yes	Yes	$\{1,1\}$	$\psi p_V p_R$
Yes	No	$\{1,0\}$	$\psi p_V (1-p_R)$
No	Yes	$\{0,1\}$	$\psi (1-p_V) p_R$
No	No	$\{0,0\}$	$\psi (1-p_V) (1-p_R) + (1-\psi)$

Table 2.2. Likelihood for all possible scenarios in a 2 species case

Scenario			Data	Likelihood
Sighting	Response	Species	$x_{i.}$	$L(x_{i.} p_{ocA}, p_{ocB}, p_{VA}, p_{VB}, p_{RA}, p_{RB})$
Yes	Yes	A	$\{1,1\}$	$\psi_A p_{VA} p_{RA}$
Yes	No	A	$\{1,0\}$	$\psi_A p_{VA} (1-p_{RA})$
No	Yes	A	$\{0,1\}$	$\psi_A (1-p_{VA}) p_{RA}$
Yes	Yes	B	$\{2,2\}$	$\psi_B p_{VB} p_{RB}$
Yes	No	B	$\{2,0\}$	$\psi_B p_{VB} (1-p_{RB})$
No	Yes	B	$\{0,2\}$	$\psi_B (1-p_{VB}) p_{RB}$
No	No		$\{0,0\}$	$\psi_A (1-p_{VA})(1-p_{RA}) + \psi_B (1-p_{VB})(1-p_{RB}) + (1-\psi_A-\psi_B)$

Figures

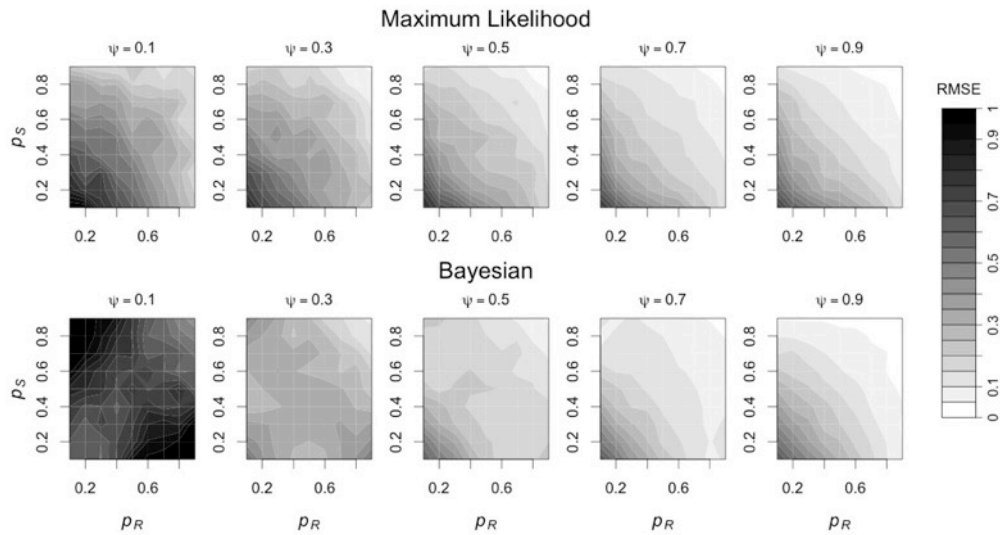


Figure 2.1. Standardized RMSE of estimates of population size for Maximum Likelihood and Bayesian estimation for the simulated plots under a variety of parameters.

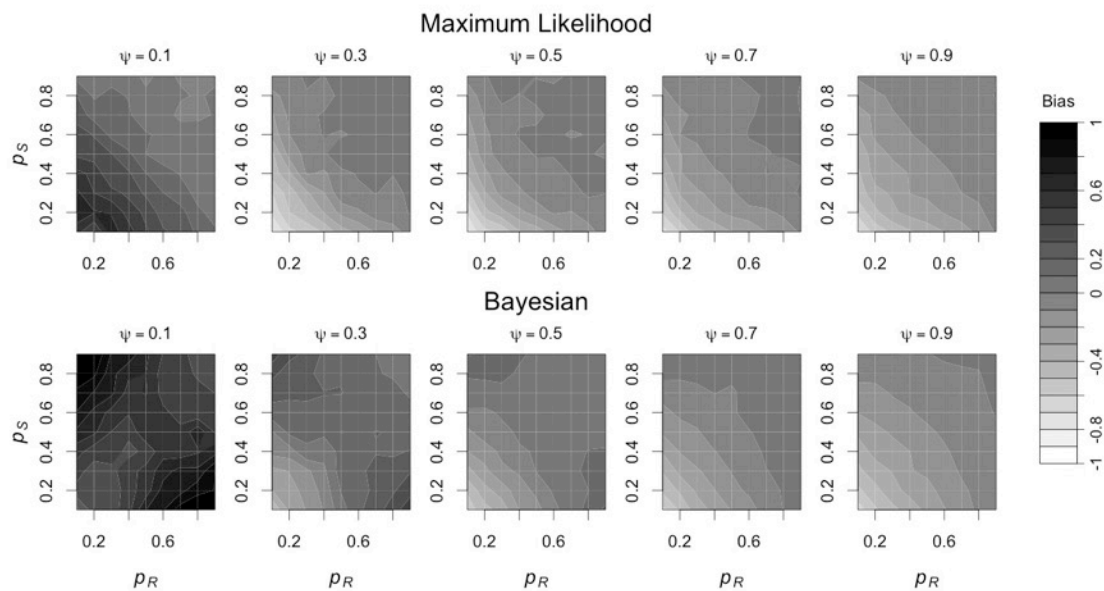


Figure 2.2. Relative bias of estimates of population size for Maximum Likelihood and Bayesian estimation for the simulated plots under a variety of parameters.

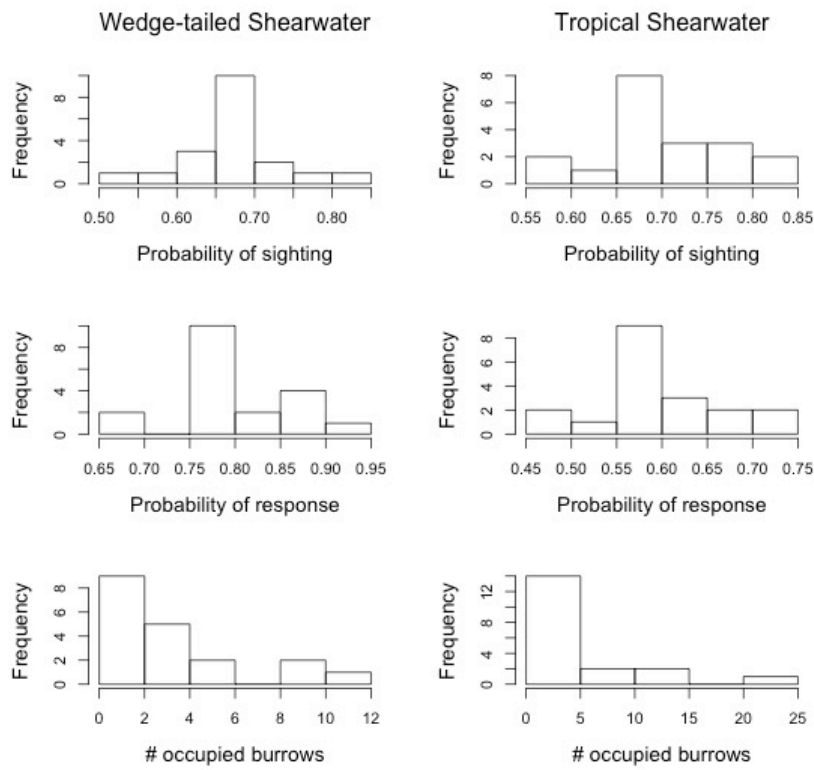


Figure 2.3. Histograms of estimated probabilities of sighting p_v , probabilities of response p_r and number of occupied burrows for the 19 sampled plots.

External Supplementary Materials (ESMs)

Table ESM1. Model selection for Aride Island's two-species shearwater census. (z) denotes plot variation in the detection parameter, while (.) denotes constant detection rates for all plots.

Model		DIC	ΔDIC
<i>P.pacificus</i>	<i>P.bailloni</i>		
$p_R(z), p_S(z)$	$p_R(z), p_S(z)$	627.51	0.00
$p_R(z), p_S(z)$	$p_R(z), p_S(.)$	651.59	24.08
$p_R(.), p_S(z)$	$p_R(.), p_S(z)$	654.40	26.89
$p_R(z), p_S(.)$	$p_R(z), p_S(.)$	657.09	29.58
$p_R(z), p_S(z)$	$p_R(.), p_S(z)$	662.37	34.86
$p_R(z), p_S(.)$	$p_R(z), p_S(z)$	665.58	38.07
$p_R(z), p_S(.)$	$p_R(.), p_S(.)$	666.35	38.84
$p_R(.), p_S(z)$	$p_R(z), p_S(z)$	666.66	39.14
$p_R(.), p_S(z)$	$p_R(.), p_S(.)$	682.89	55.38
$p_R(z), p_S(z)$	$p_R(.), p_S(.)$	684.58	57.07
$p_R(.), p_S(.)$	$p_R(.), p_S(z)$	684.93	57.42
$p_R(z), p_S(.)$	$p_R(.), p_S(.)$	686.40	58.89
$p_R(.), p_S(.)$	$p_R(z), p_S(z)$	688.23	60.71
$p_R(.), p_S(z)$	$p_R(z), p_S(.)$	695.90	68.39
$p_R(.), p_S(.)$	$p_R(z), p_S(.)$	702.62	75.11
$p_R(.), p_S(.)$	$p_R(.), p_S(.)$	713.44	85.93

Table ESM2. Parameter estimates for Aride Island's two-species shearwater census. The best model includes variation in occupancy, sighting and response probabilities for both species

Parameter	Mean Estimate	SD
Wedge-tailed Shearwater		
μ_{ψ}	-1.224	0.471
σ_{ψ}	1.109	0.534
μ_{ps}	0.948	0.349
σ_{ps}	0.909	0.615
μ_{pr}	2.011	1.067
σ_{pr}	1.656	1.620
Tropical Shearwater		
μ_{ψ}	-0.493	0.869
σ_{ψ}	3.107	1.184
μ_{ps}	0.201	9.875
σ_{ps}	4.994	2.890
μ_{pr}	4.431	0.384
σ_{pr}	0.754	0.471

CHAPTER 3

Assessing population size in nocturnal dwelling seabirds accounting for detection probability and habitat preferences: a sequential approach

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Manuscript under review: Calabrese L., Le Rest K., Rocamora G., Bretagnolle V. (under review). Analysis of playback census to estimate the density of cavity-dwelling birds. Biological Conservation.

Abstract

Determining the abundance and distribution of nest-burrowing seabirds has always been challenging. Here, we propose a sequential approach that accounts for incomplete detection and habitat selection to estimate population size. We use double detection (visual and acoustic) in each sampling area and we propose two methods to calculate the number of breeding pairs, one correcting for response rate and the other for both response rate and breeding failure. A habitat selection model is subsequently implemented within a spatio-temporal framework using Integrated Nested Laplace Approximation. We apply this method to the tropical and the wedge-tailed shearwaters breeding on Aride Island Nature Reserve (Seychelles) using census data of three consecutive years. We found that both species prefer medium-high slope and low vegetation. The wedge-tailed selects also areas with deep soil. The wedge-tailed shearwater population resulted to be about 15,000 pairs (97.5% confidence interval 12,000-19,000), while the tropical was estimated to be about 23,000 (19,000-29,000), reaching 30,000 pairs when accounting for breeding cycle in this latter species. These estimates are in line with previous results for the first species and suggest a steep decline of the latter. In view of our results, to improve the conservation of the two species, we suggest vegetation management and a targeted anti-poaching vigilance in the most populated areas. Our research provides an example of how technology and statistical improvement in tracking lifestyles can increase our understanding of the ecology and status of species that are difficult to study to the ultimate benefits of management and conservation.

3.1 Introduction

As top predators, seabirds are a major component of marine ecosystems (Gaston 2004; Schreiber and Burger 2001). They have been much studied in regard to marine ecosystems functioning (Frederiksen et al. 2006; Furness and Camphuysen 1997; Zador et al. 2013) and used to evaluate the impact of climate change (Barbraud and Weimerskirch 2001; Barbraud et al. 2008), fisheries (Catry et al. 2009b; Einoder 2009; Le Corre et al. 2012) and as indicators of prey stock (Le Corre and Jaquemet 2005; Lyday et al. 2015; Montevecchi 1993; Piatt et al. 2007). Knowledge about seabirds is also essential for conservation purposes (Bibby et al. 2012). In particular, changes in numbers and range can be analyzed in relation to environmental features, direct threats (e. g. poaching of adults, young and eggs) and success or failure of conservation management policies in protected areas (Bibby et al. 2012; Sutherland et al. 2004).

However, producing accurate estimation of population parameters has proved extremely difficult, especially for nocturnal nest-burrowing seabirds such as petrels or auklets (Scott et al. 2009; Spear et al. 1995; Warham 1996). This is mainly because: i) the breeding sites are often inaccessible (remote islands, steep slopes, mountain tops); ii) fieldwork needs to be conducted at night (i.e. when most breeding birds are present and more easily detectable); iii) breeding birds can occupy deep burrows, making it difficult for their presence to be assessed; iv) several species breed usually within the same colony, with different breeding cycles or habitat preferences (Hunter et al., 1982); v) accounting for breeding failures and non-breeders is uneasy although the latter can represent the majority of the population (Furness and Birkhead, 1984; Warham, 1996). Not surprisingly therefore, many census techniques have been attempted for nest-burrowing seabirds, but only a few accounting for imperfect detection and habitat selection (Borchers et al. 2002; Thompson 2002; review in Rayner et al. 2007; Whitehead et al. 2014.).

Habitat preferences can be accounted for by using 'species distribution models' (SDMs). SDMs have been increasingly used in the last three decades (Guisan and Thuiller 2005; Guisan and Zimmermann 2000) and have been successfully applied on plants and animals censuses, though only fairly recently on seabirds (Olivier and Wotherspoon 2005; Rayner et al. 2007; Whitehead et al. 2014). SDMs enable the production of species suitability maps based on habitat preferences under the habitat selection paradigm (Jones 2001). However, using SDM implies that the number of breeding pairs is known without bias at sampled locations, a rare case indeed in burrowing seabirds, especially for those breeding in long winding tunnels or boulder areas. Detectability therefore must be taken into account and improved, e.g. by using both visual and acoustic detection (Barbraud and Delord 2006; Betts 1998; Burger and Lawrence 2001; James and Robertson 1985; Ratcliffe et al. 1998; Soanes et al. 2012; Warham, 1996). Combining correction for detection with species distribution models appears to be the best solution for providing reliable estimates of distribution, abundance and trends for these species.

Here we propose a sequential approach to assess habitat preferences and abundance of nest-burrowing seabirds, which accounts for species detectability and habitat preferences within a spatio-temporal modelling framework. The proposed methodology is applied on two burrow-nesting shearwaters, the tropical shearwater *Puffinus bailloni* and the wedge-tailed shearwater *Puffinus pacificus*. Both species breed in the Seychelles archipelago, where economic interests (that generate a high level of

anthropic activity) overlap with biodiversity hotspots which are often subject to anthropic, climatic and other threats. Results obtained for these two species are discussed and management actions suggested.

3.2 Material and methods

Study site

The Seychelles hosts some of the largest seabird populations in the Indian Ocean and harbours no less than 20 terrestrial Important Bird Areas of which 12 have been classified predominantly for their seabird colonies or congregations (Rocamora and Skerrett 2001). The Seychelles waters are also targeted by commercial fishing, which represents its second largest economic activity (Critical Ecosystem Partnership Fund 2014). For example in 2010, c. 60 metric tonnes of tuna were caught in the Seychelles Economic Exclusive Zone (Seychelles Fishing Authority 2014) representing 1.4 % of the world tuna catch (<http://www.fao.org/fishery/statistics/tuna-catches/query/en>). In addition, offshore waters are dedicated to oil exploration as indicated in the model petroleum agreement 2013 (www.petroseychelles.com). Finally, coral bleaching in the Seychelles has been the focus of repeated alerts since 1998 (Obura et al. 2008; The Seychelles National Climate Change Committee 2009) indicating an increment of sea surface temperature.

Our study was carried out on Aride Island (4° 12' 46"S, 55° 39' 53"E; see Figure 3.1a for location), a rat-free island declared as a nature reserve in 1975 (Warman and Todd 1984). It is the northernmost granitic island of the Seychelles archipelago and has a surface of c. 73 ha, of which only c. 7 ha are flat (plateau), with a maximum height of 135 m asl (Warman and Todd 1984). The island hosts the largest seabird population of the Seychelles granitic archipelago, with 10 seabird breeding species (Rocamora and Skerrett 2001). Despite the fact that previously Aride had been described by sailors as a speck of bare rocks in the ocean, the island is now almost completely covered with trees and the native *Pisonia grandis* is the most dominant species. Relictual surfaces of 'glades' dominated by herbaceous plants and surrounded by bushes, are also present. The north side of the island is the steepest, while a small ridge expands from east to west.

Study species

The tropical shearwater is one of the smallest species in the *Puffinus* genus (c.200 g; Brooke, 2004). Its range includes the tropical Indian and Pacific Oceans where different subspecies occur (del Hoyo et al. 2014). In the Western Indian Ocean, it is found on Réunion Island (subspecies *bailloni*) and on the Seychelles archipelago (subspecies *nicolae*) with small colonies also on Comoros and Maldives (Bretagnolle et al. 2000). Its breeding biology, foraging behavior and ecology are poorly known, and the colony of Aride is possibly the largest colony in the world (del Hoyo et al. 2014; Skerrett et al. 2001). Most colonies have been severely impacted by rats, which led to extinctions on several of the Seychelles islands (e.g. D'Arros Desroches and Marie-Louise) although small numbers still breed sporadically on some rat infested islands including Mahé (at c. 600 asl) and Marianne Islands (G. Rocamora 2012 pers. obs.). Yet, the species has recently been assessed as Least Concern under the IUCN Red List Category (BirdLife

International 2014). Estimating tropical shearwater population size is notoriously difficult, and indeed no accurate world estimates, nor trends, are available.

The wedge-tailed shearwater is twice as large (c. 400 g) and monotypic, with a breeding range extending throughout the tropical and subtropical latitudes of the Pacific Ocean, including the east coasts of Australia, New Caledonia and Polynesia, and the Indian Ocean (Brooke 2004; del Hoyo et al. 2014; Harrison 1983). It has been well documented in different breeding sites for which population estimates and trends are available (Burger and Lawrence 2001; Dyer 2003; Dyer et al. 2005; Kappes et al. 2013). It is classified as Least Concern (BirdLife International 2012) even though population trends in several localities are negative, threatened by unsustainable levels of fisheries exploitation, persecution and predation by invasive species (Brooke 2004; Dyer 2003; BirdLife International 2012). In the granitic islands, the main colonies are located on Cousine (considered the largest colony), Aride and Cousin (Rocamora and Skerrett 2001). The largest colony of the outer islands is on St Joseph atoll, in the Amirantes (Kappes et al. 2013). Smaller colonies are found on Ile aux récifs, Mamelles and other smaller granitic islets, and also on other coralline islands (e.g. Bird Island, D'Arros, Desnoeufs, Marie-Louise; Skerrett et al. 2001).

The two studied species share the same breeding habitat, but strongly differ in their size, hence in their ability to compete for burrows, and in their breeding phenology. The tropical shearwater breeds all year round while the wedge-tailed shearwater breeds synchronously between September and March. Population size estimates for both species are available for Aride Island since 1979 (Table 3.3), but until 1998 the survey methods were only based on burrow counts without accounting for burrows occupancy. Afterwards, even if an implemented protocol accounting for burrow occupancy was put in place (Betts 1998), the surveyed area (0.27 % of the island) was not large enough to provide a reliable population size. In addition, data analysis did not account for the simultaneous presence of the two species and for habitat selection.

Habitat mapping

No habitat map was available for Aride Island at the time of the survey. However, two intertwined grids oriented N-S of about 100 x 100 m were set up in 2004 and 2005 across the whole island for monitoring purposes based on systematic sampling, in particular to conduct habitat and seabird surveys (Evans and Hobro 2005). The grid consists of 210 points spaced at c. 70 m from each other oriented NE-SW. Tree, shrub, rock, herb and bare ground covers (in %), canopy height and soil depth were measured at the 210 grid points (see Table 3.1). An additional 93 randomly selected plots were added to increase the quality of the habitat maps. Habitat distributions were thus obtained from the 303 sampled points (Figure 3.1b) using inverse distance weighting interpolation (IDW). An accurate altitude map was built using 1500 points manually digitalized from a 1:25,000 georeferenced map. Exposure and slope were computed from the altitude map (using R package "Raster", R Development Core Team 2014). Interpolated habitat maps are presented in the Appendix A, together with slope and altitude maps.

Shearwater census

Field surveys were carried out over the whole island by sampling circular plots of 100 m² within different types of habitat. In total, 150 plots were surveyed from 2011 to 2014: 19 in 2011-2012, 60 in 2012-2013, and 150 in 2013-2014 (including the 60), of which 19 were surveyed regularly for shearwater census since 1996 (Sampson and Sampson 2007). Plots added to the 19 original ones were selected randomly from the 210 grid points used for the habitat mapping so that they reflected well the habitat space (see Appendix B). In 2013-2014, the 150 sampled plots represented 2.05% of the island surface, i.e. just above the minimum required for an expected meaningful sample (Brashares and Sam 2005).

The shearwater census was carried out during a period which included the breeding season of the wedge-tailed shearwater and the two major breeding peaks for the tropical shearwater. To increase detection rate, both playback and a borescope were used. The field protocol described by Betts (1998) was taken as a baseline. During the two breeding seasons 2011-2012 and 2012-2013 (from now on indicated as 2012 and 2013 seasons respectively) the censuses were carried out in November, February and May. In the 2013-2014 season (from now on indicated as 2014 season), plots were visited only once between November 2013 to March 2014. Plots were always visited at night, from 08:00 PM to 01:00 AM by 2-4 persons, depending on staff availability. As a first step, the plot was delimited, and every single entrance (i.e., potential burrow) lying partly or entirely in the plot was recorded. Each potential burrow or cavity area was first inspected visually with a torch or, if winding or too deep, with the help of a plastic pipe or a borescope (Potensic® Digital Endoscope Borescope" 3.5" LCD Monitor 6 Leds Night Vision) (McKechnie et al., 2007; Scott et al., 2009). Visual check of the burrow allowed classifying cavities as: i) truly empty (i.e. entirely visible and empty), ii) empty but with the presence of breeding signs, e.g. predated or broken egg, dead chick, adult feathers, down or other signs of breeding, iii) occupied by either an adult, a pair, an adult on egg, a downy chick, a downy chick with some feathers or a fully feathered chick. This left a remaining category of burrows with unknown content, which could be either truly empty or occupied by one of the two species. After all burrows were visually checked, burrows with unknown content as well as occupied burrows were played-back with a tape-lure (Rocamora et al. 2000) with an MP3 player connected to a iHOME (model iBT16) speaker. Sound volume matched (by ear) that of a typical loud shearwater. When burrow occupancy was known, only the species call (including both single birds and duets) was played for 1:24 minutes for tropical and 1:58 minutes for wedge-tailed. For burrows of unknown status, calls of both species were played (for 3:22 minutes in total). The tape was stopped c.5 seconds every 15-20 seconds for tropical and 30 seconds for wedge-tailed (Burger and Lawrence 2001) to allow the detection of low answers. All occupied burrows were permanently marked with a unique number using a coated iron wire tying a plastic cylinder fixed at the entrance of the burrows using roots or natural items.

Calculating the number of pairs per sampled plot

To obtain an unbiased number of pairs per species and per plot, we need to account for the content of invisible burrows, detection rate and breeding failure, i.e. treating i) the burrows that could not be visually inspected and for which no response was obtained after playback, and ii) the currently empty burrows, that may have contained a pair

earlier in the season (e.g. premature failures) or not. We used two different methods: in the first method, census data were integrated within a Bayesian statistical framework (see CHAPTER 2). This method accounts for the imperfect detection based on response rate to playback in order to calculate the probability of occupancy. This probability is then used to estimate the number of burrows with unknown content (content not visible and no response to the playback) that are occupied by one or the other species. However, while accounting for imperfect detection, this method does not account for breeding failures. Therefore in our case, the resulting estimates correspond to a minimum population size for the 2014 census.

To account for breeding failure in both species we used a second method that considers the data collected during the three breeding seasons. To estimate which proportion of empty burrows results from breeding failure, we took into account time (since total number of breeding failure will increase with season) and location in the island (as spatial variation in breeding density of the two species might occur). We assumed that the plots surveyed at the beginning of the breeding season (November) were at the maximum occupancy rate. Data were available in November (all years combined) for 73 plots and were used to map (using inverse distance weighting interpolation) the relative proportions of wedge-tailed, tropical shearwaters and empty burrows for the whole island, at a 1 ha resolution (see Appendix C). Then, we used the following procedure to calculate the number of pairs per plot accounting for imperfect detection, breeding failures and coexistence of the two species (i.e., an unknown burrow cannot be occupied simultaneously by the two species). The logic used in the calculation is described in details in Appendix C (which discusses also the assumptions used), a summary is provided below. The total number of burrows is obtained for tropical (TS) and wedge-tailed shearwater (WS) using the following formula (see Figure 3.2 for explanations on the various counts, N1 to N20):

$$\text{TOT TS} = N1 + N4 + N14 + N7 + N16 \quad (\text{EQN 1})$$

$$\text{TOT WS} = N2 + N5 + N13 + N8 + N15 \quad (\text{EQN 2})$$

$$\text{With } N13 = N10 * Pws_t \quad (\text{EQN 3})$$

$$N14 = N10 * Pts_t \quad (\text{EQN 4})$$

$$N7 = N4 [(1 - y_T) / y_T] \quad (\text{EQN 5})$$

$$N8 = N5 [(1 - y_W) / y_W] \quad (\text{EQN 6})$$

$$N15 = N9 * Pws_t \quad (\text{EQN 7})$$

$$N16 = N9 * Pts_t \quad (\text{EQN 8})$$

$$\text{with } N9 = N6 - N7 - N8$$

where N1 and N2 are the number of tropical and wedge-tailed pairs visible respectively, N4 and N5 the number that were not visible but responded to the play-back, N14 and N13 are the estimated portion of visible burrows that were empty due to failures, N7 and N8 are the estimation of number of pairs present but not detected (not visible burrows with no response but bird present) and N16 and N15 are the portion of invisible (unknown) empty nests which are empty due to failure. y_T and y_W are respectively response rates of tropical and wedge-tailed to playback according to seasonal variation, and Pts_t and Pws_t are the proportion of both species among all visible burrows across the island in November. N1, N2, N4, N5, N6, N10, N11, N12, N16, N17, N19 & N20 are directly available from the field data. See Appendix C for calculations of all equations.

Species habitat and spatial models

The count data were modelled using a negative binomial distribution to account for over-dispersion (Richards 2008). The candidate habitat variables were checked for collinearity. The highest Pearson correlation obtained was 0.5, thus lower than the limit of 0.7 (Dormann et al. 2013), indicating that all variables could be used in the same model. Habitat variables were selected using the Akaike's Information Criterion (Appendix D) (Zurr et al. 2013). A step-wise selection procedure starting from the full model (i.e. including all the habitat variables) was applied to identify the best model. A choice among interactions and quadratic variables was first done separately and the significant ones were added to the full model (Zurr et al. 2013). This variables selection step was performed using only the 2014 data. It was therefore simplified by eliminating the presence of replicates (in 2012-2013) while maximizing the number of data, thus avoiding using a random factor for the plot identity.

Once habitat variables were selected, they were implemented in a spatio-temporal explicit model to estimate the population abundance and distribution of the two species. The model included the habitat variables as fixed effect and a random spatio-temporal term in order to account for spatio-temporal dependences. Model parameters were estimated using the Integrated Nested Laplace Approximation (INLA, see Rue et al., 2009). INLA allows estimating complex Bayesian hierarchical models in low computation times. (Carson and Flemming 2014; Muñoz et al. 2013; Rue et al. 2009). For continuous spatial modelling, the stochastic partial differential equation approach (SPDE) is preconized. It consists in using another approximation making the estimation of Gaussian random fields (a random field correspond to a random variable having a spatial structure) of the Matérn class much easier (Lindgren et al. 2011). Such approach requires defining a constrained Delaunay triangulation, which was done in such a way to keep the distance between the nodes lower than 10 m (see Appendix E). As the data set is composed of three distinct years of sampling, a temporal term was also added to the spatial structure. The temporal term chosen was an autoregressive order 1 structure (Blangiardo et al. 2013; Cameletti et al. 2013), which can be interpreted as the correlation of the random field at a given location between year t and $t-1$. The three years of sampling (2012, 2013, 2014) were used as time steps and the data collected in May 2012 and 2013 were removed in order to have a more homogeneous time period within each time step (from November to March). INLA is available in the R software (R core team, 2014) with the package R-INLA (www.r-inla.org). Predictions were made on a grid of resolution 10 x 10 m covering the whole island except the rocky coastal areas since shearwaters could not dig burrows in these areas, and were, indeed, totally absent.

3.3 Results

Species habitat preferences

The two methods used to account for detection rate yielded different numbers of pairs per plot, since the first method did not account for breeding failure, conversely to the second. Indeed, estimated numbers in method 1 were lower for both species but the two methods were nevertheless strongly correlated to each other ($R^2 = 0.96$, for tropical and $R^2 = 0.97$, for wedge-tailed, $n=150$ plots, $p < 0.001$). Habitat models were fitted from the total number of predicted occupied burrows for the two species, as estimated by either

method 1 or 2. As expected, the date, which was highly significant for wedge-tailed using estimates from method 1 was no longer significant with method 2 as the effect of time was already taken into account in the formula (breeding failure, see Appendix C). Contribution of individual variables, model coefficients, explained variance and standard errors for the selected model for each species are shown in Table 3.2. Significant habitat variables were identical, for both species, irrespective of the method used, but did differ between species (Table 3.2). The number of pairs per plot for both species was positively correlated with slope and shrub. The abundance of wedge-tailed was also positively correlated with soil depth and rock cover.

Prediction maps and total abundance

For the spatio-temporal modeling, we retained values obtained within the second method, since our goal was to predict breeding numbers irrespective of breeding failure. Results for the wedge-tailed and tropical shearwater are shown in Figure 3.3 (standard errors maps are provided in Appendix F). As distribution for the two species over the three year time period was comparable, we decided to show only the map for 2014, this being the season with a larger sample size. The distribution of breeding pairs across the island was more homogeneous for tropical than for wedge-tailed shearwater (Figure 3.3), since breeding pairs of the former were present also on flat areas while the latter was mainly found on the hill or on steep areas (see also maps in Castle and Mileto, 1991 indicating presence/absence of the species). The temporal correlation between the three surveys for both tropical and wedge-tailed were very high: 0.98 and 0.97 respectively, suggesting highly similar distribution of the breeding pairs among the three years, which could indicate that the birds (not necessarily the same ones) choose to breed in the same areas during different breeding seasons. The spatial autocorrelation slightly differed between the two species, but variance stabilized at rather short distances: 196 m for the wedge-tailed and 88 m for the tropical.

The total abundance during the seasons 2012, 2013 and 2014 were comparable, with 14,977 (97.5% confidence interval 11,914-19,715), 14,848 (12,340-18,969) and 14,297 (11,891-18,152) pairs of wedge-tailed and 23,142 (19,119-29,634), 22,660 (18,738-28,523) and 22,610 (18,861-28,518) breeding pairs of tropical shearwaters respectively. In tropical shearwater, these values must be considered as lower bound values, since we could not totally account for breeding failure in this species as the survey did not cover the whole breeding season (being a year-round breeder) therefore the maximum occupancy rate (intercept) cannot be identified. Furthermore, the breeding season for this species only extends to 9 months and multiple pairs occupy the same burrow within one year. Applying a 4/3 multiplication coefficient (accounting for 9 months out of 12) suggest that 30,000 breeding pairs must be a more reliable mean estimate for the tropical shearwater on Aride Island, twice the numbers of wedge-tailed 15 000 pairs).

3.4 Discussion

Species management strategies rely on accurate estimates of baseline population sizes, which can be used to analyze the responses of populations to perturbations or management decisions. Nest-burrowing seabirds have been particularly difficult subjects in this regard (Scott et al., 2009; Spear et al., 1995; Warham, 1996). By applying a repeatable design and a performing and innovative census method and analysis, we show that it is possible to obtain precise estimations for the number of breeding pairs. This will allow the detection of future changes in population size and trends, as well as enhancing the reliability of our understanding of habitat preferences in view of making sound management decisions.

Estimating population size accounting for detectability, breeding failure and habitat preferences

The method proposed here may be applied to any burrowing seabird, breeding in mixed or mono-specific colonies, showing a response to a tape-lure, or in general, for which a double detection method can be applied (e.g., a visual and an acoustic one). Many authors have already proposed methods to overcome the problem of the detection rate whether applying SDMs to the results or not (review in Rayner et al. 2007, Whitehead et al. 2014). For example, as many studies suggested, a sub-sample of burrows belonging or not to the sampling area could be checked regularly to obtain the proportion of burrows occupied or the detection probability to be applied at the number of occupied burrows detected in the whole sampling area (see for example Whitehead 2014). These methods, however, do not account for differences in occupancy rates in different areas given by the spatial structure of the colony.

The novelty of our method relies in calculating the number of breeding pairs by correcting for both detection error (depending on whether double detection approach is used) and breeding failure. Then, habitat preferences are investigated by using a SDM accounting for spatio-temporal autocorrelation. The spatial term acknowledges the presence of spatial features not included in the habitat variables, e.g. the social behavior of colonial seabirds that drives individuals to cluster (Schreiber and Burger 2001), which improves prediction of the species distribution. The temporal term allows for the consideration of different sampling seasons (different successive years) within the same model and links them such that the abundance at time t can affect its abundance at time $t+1$. Therefore, our sequential approach allows estimating population abundance and distribution, as well as temporal dynamics, while accounting for major problems when analyzing nest-burrowing seabird data. Depending on whether surveys are spread all over the breeding season or concentrated at the beginning (i.e., depending on the amount of work and the available workforce), we also propose two different methods for accounting for detection rate, one of which further accounts for breeding failure. The first method can be used if the census is carried out at the beginning of the breeding season (minor risk of failures). The second method can be used if the census needs to be undertaken across the breeding season. Indeed, when breeding failure is not accounted for, and the fieldwork is carried out throughout the whole breeding season, the obtained estimates are 37% and 44% lower for tropical and wedge-tailed, respectively.

Shearwaters of Aride Island: Abundance, distribution, habitat preferences and trends

Both species select relatively steep areas for burrows excavation, which is in accordance with the findings of other studies on petrels, where steep slopes were selected to enable an easier take off and also serves as an anti-predatory strategy (Brooke 2004; Vanzandt et al. 2014; Warham 1996). For example, the tropical shearwaters at Réunion Island breed in very steep areas, mainly cliffs (Bretagnolle et al. 2000). However, on Aride and more generally in the Seychelles, this species can also be found breeding on flat ground (Burger and Lawrence 2001) as the individuals have developed the ability to climb trees which enables take off. This behavior could allow the species to be less selective towards steeper areas (if breeding in forest) in comparison with the wedge-tailed, for which the climbing behavior has never been recorded. The presence of both species is also positively correlated with shrub coverage, indicating a preference for lower vegetation cover that presumably also allows for easier take-off. Moreover our results show that the wedge-tailed shearwater is strongly influenced by soft soil depth, which is in accordance with other studies carried out in other Pacific Ocean islands (Dyer and Hill 1992). The percentage of rock cover has a slightly positive effect on the number of wedge-tailed breeding pairs. In fact, this species often digs burrows under big rocks and uses natural cavities in boulder-dominated areas, as also recorded in other studies (Brooke 2004; Burger and Lawrence 2001). The effect of altitude on both species was insignificant even if for other petrel species it seems to be a relevant feature for the distribution and abundance of breeding pairs (Bretagnolle et al. 2000; Oka et al. 1996; Rayner et al. 2007; Scott et al. 2009; Whitehead et al. 2014). However, given the limited maximum altitude of Aride (135 m) this result is not surprising. Overall, the wedge-tailed seems to be more selective than the tropical shearwater in terms of habitat.

Data for both species have been collected on Aride since 1979. Table 3.3 shows population estimates, survey and analysis methods applied for each study. Previous surveys were indeed limited in terms of accuracy and precision; however, they can be used to analyse the species trends. Table 3.3 also includes 2012 and 2013 estimates using only the 19 plots surveyed since 1996 and the same method (Betts 1998) to allow direct comparison. The “old method” (Betts 1998) clearly overestimates the tropical shearwater population size, while being more reliable for the wedge-tailed shearwater. In 2012, the old method predicts a population size of 54,000 pairs of tropical shearwaters (compared to 23,000 with our method), i.e. an overestimate of 2.3 factor, while it is less with 2013 data (overestimate of 1.5 factor). No figure could be drawn for 2014 since only one round was performed, and data could therefore not be compared. Despite the fact that we cannot infer correctly the numbers present before 2012, the same 20 (only 19 since 2011 as one plot was lost) plots were monitored over 16 years (at irregular intervals), and the trend obtained from this subsample indicates a decreasing population number of 40% for the tropical, and a stable population for the wedge-tailed. The reasons for these trends are not entirely clear: one possible reason may be related to vegetation changes, since Aride used to be forest free, and is now mostly forested. The vegetation was indeed strongly influenced by anthropogenic modification, as it was managed as a coconut plantation (mainly on its plateau) until 1973. Moreover, the area of the hill not occupied by coconut trees was kept clear from vegetation to allow sooty terns (*Onychoprion fuscatus*) to breed in large numbers for egg harvesting (Feare 1976). Vegetation surveys done on Aride since the 1970s (Castle and Mileto 1991; Sampson and Sampson 2007; Warman and Todd 1984) have shown a

decrease in the number of glades and their total area. Most open areas have been naturally replaced by canopy cover dominated by the native species *Pisonia grandis*. The area covered in fern (native species *Nephrolepis biserrata*) has also increased, reaching up to 1.5 m height in thick patches. The development of more dense vegetation leaves less space for bare soil and rocks and it can therefore become an issue for both burrow-nesting shearwaters and ground-nesting/feeding birds species (Skerrett et al. 2001). Moreover, tropical shearwater may suffer from competition with the wedge-tailed which have been proved to be more dominant than other seabird species in mixed colonies (see also Villard et al. 2006). Indeed, the wedge-tailed shearwaters dominate smaller co-existing species, digging their burrows and competing for the best nesting sites (Catry et al. 2009b; Dunlop et al. 2002; McClelland et al. 2008).

Aride population of the tropical shearwater is confirmed as the largest single colony known worldwide, though detailed counts are available only for a tiny proportion of the colonies around the world. Only the population breeding on the entirety of the Phoenix Islands may be larger (10,000-100,000 in Thibault and Bretagnolle 1999). Within the Indian Ocean, the Aride population is about 75% of the entire population, making its decline particularly worrying from a conservation point of view. Other significant populations are on Cousin & Cousine Islands, Seychelles, with about 1,500 pairs (based on information from Nature Seychelles 2014) (5,100 based on Burger and Lawrence 2001) and a few hundreds pairs respectively, and on Réunion Island, with 3-5000 pairs (Bretagnolle et al. 2000), but their trends are uncertain. The population of wedge-tailed shearwaters on Aride is less significant when compared to other locations.

Conclusions and conservation implications

To conclude, given the sudden decline of tropical shearwater, there is the need of management actions orientated to its conservation at the colony level.

In terms of habitat management, to favor the two species it might be relevant to keep the glades open since they are preferred habitats for other conservation dependent species, e.g. Roseate terns *Sterna dougallii* (Ramos 1998). As a management trial, moderate clearing of the vegetation in selected dense colony areas with high *Pisonia grandis* may be considered. As already documented, *Pisonia* sticky seeds can heavily affect shearwaters and other ground-nesting birds (making individuals unable to fly; see Burger 2005; Wade 2010). Aride (as the other neighboring protected islands) witnessed a very fast dispersion and growth of *Pisonia grandis*, after its vegetation was no longer cleared to favor ground-nesting terns. The clearing trial might reveal a preference of tropical shearwaters in areas without high canopy cover and eventually may help in assessing the impact of *Pisonia* on the shearwater population. However, this would require the continuous monitoring and census of the colony, an effort that appears compulsory given the observed decline of this species in the largest colony of the world. Conversely, managing the vegetation may be slightly disadvantageous to the wedge-tailed, therefore favoring the tropical (assuming competition truly happens), since the wedge-tailed prefers deep soils that are formed by high *Pisonia* trees.

Although harvesting of birds and eggs for human consumption became illegal in 1973 in the Seychelles, poaching for shearwaters and sooty terns (both adults, chicks and eggs) is still ongoing in significant parts of the seabird colonies. Poachers usually come at night to the north side of Aride and land on rocks in the more accessible areas. This annual practice is likely to have an impact on the distribution and number of

breeding pairs in areas exploited by poachers, which is more likely to be inhabited by tropical shearwaters, since it is more widespread than the wedge-tailed. In general, the north-west and the north-east sides of the hill have lower densities than the surrounding areas, possibly because they are easy landing sites for poachers. For the conservation of the shearwaters, as well as other species, an intense anti-poaching activity is strongly recommended, in particular during the wedge-tailed shearwater and sooty tern breeding seasons (June-September) since there is clear evidence of poacher activity all over the island during this period.

3.5 Acknowledgements

We would like to acknowledge all the Aride team members and volunteers that participated to the night field work, in particular the Assistant Conservation Officers Gwen Maggs. Alejandro Anganuzzi and Marco Girardello provided statistical advices, Alexander Coles helped with the English revisions and Adrian Skerrett gave very meaningful advice and technical support. This research was sponsored by the Island Conservation Society, CNRS Chizé, Fondation d'entreprise TOTAL, James Cadbury foundation and Fundació Miguel Torres. This research was approved by the Seychelles Bureau of Standards (Research Permit N°A0157). We wish to thank Seychelles authorities and all the organizations and individuals that have helped to obtain the permit.

Tables

Table 3.1. Habitat features measured on the field with a description of methods. The sum of the features with^(a) gives 100% while the others are independent among each other.

Variable	Unit of measure	Habitat characteristic measured							
		Description	Tool	Accuracy	Average	Standard deviation	Median	Minimum	Maximum
Tree	%	percentage of vegetation cover > 5m	visual estimation	-	70.91	27.98	80	0	100
Shrub	%	percentage of vegetation cover < 5m	visual estimation	-	22.72	19.79	20	0	90
Rock *	%	percentage of rock including boulders areas and small rocks areas	visual estimation	-	48.17	30.52	45	0	100
Herb *	%	herb cover, most of the time resulting in <i>Nephrolepis biserrata</i>	visual estimation	-	23.17	29.89	10	0	100
Bare ground *	%	percentage of bare soil	visual estimation	-	28.66	27.44	20	0	100
Soil depth	cm	average of four measurements taken at the 4 cardinal points at the edge of the 5.65 m rope; if rocks were present at the measuring point, the measurement was taken at the nearest suitable point	gratuated stick	1 mm	12.12	5.3	11.6	0	27.4
Slope	grade	measurement taken from one end of the circumference of the plot to the other, passing through the center with at the maximum slope	clinometer and two measuring poles	0.1 grade	22.63	11.45	23.28	0.09	59.71
Altitude	m	average accuracy 10 m	GPS GARMIN 62s	average 5 m	42.18	31.28	40	0	130
Exposure	cardinal point	recorded at the center of the plot	compass	-	-	-	-	-	-

Table 3.2. Selected variables of the habitat models for wedge-tailed and tropical shearwater. Standardized coefficients, standard errors and p values are provided.

Species	Variable	Standardized Coefficient	Standard error	P value
Method 1				
Wedge-tailed S.	Shrub	0.28271	0.12733	< 0.05
	Rock	0.33595	0.15882	< 0.05
	Slope	0.45185	0.15692	< 0.01
	Soil	0.40274	0.13036	< 0.01
	Date	-0.45983	0.13145	< 0.001
Tropical S.				
	Shrub	0.22162	0.09343	< 0.05
	Slope	0.6676	0.10323	< 0.001
Method 2				
Wedge-tailed S.	Shrub	0.20595	0.09259	< 0.05
	Rock	0.28747	0.11305	< 0.05
	Slope	1.26009	0.36819	< 0.001
	Slope^2	-0.78513	0.33654	< 0.05
	Soil	0.40069	0.09474	< 0.001
Tropical S.				
	Shrub	0.18277	0.07456	< 0.05
	Slope	0.57521	0.08052	< 0.001

Table 3.3. Shearwaters' surveys and analysis methods applied on Aride Island (Seychelles) since the first survey in 1979.

Year	Counting Method	Analysis Method	Total Surveyed Area (Ha)	% Surveyed Area	Estimation Tropical	Estimation Wedge-tailed	Source
1979	count of all burrows	area-based	0.4	0.47	40,000	20,000	Warman & Todd (1979)
1988-89	count of all burrows	area-based	0.4	0.47	34,000	17,000	Bullock (1989)
1989-90	apply occupancy rate to data transects	area-based	0.4	0.47	10,000	21,500	Castle & Mileto (1991)
1990-91	apply occupancy rate to data transects	area-based	0.4	0.47	14,000	10,500	Castle & Mileto (1991)
1996-97	play-back in plots (3 rounds)	area-based	0.2	0.27	57,000	19,500	Betts (1998)
2003-04	play-back in plots (3 rounds)	area-based	0.2	0.27	75,000	13,668	Betts (2004)
2006-07	play-back in plots (3 rounds)	area-based	0.2	0.27	98,064	20,115	Sampson & Sampson (2007)
2011-12	play-back in plots (3 rounds)	area-based	0.19	0.26	54,844	15,902	This study
2011-12	play-back in plots (3 rounds)	habitat-based	0.19	0.26	19,119-29,634	11,914-19,715	This study
2012-13	play-back in plots (3 rounds)	area-based	0.6	0.82	34,270	16,506	This study
2012-13	play-back in plots (3 rounds)	habitat-based	0.6	0.82	18,738-28,523	12,340-18,969	This study

Figures

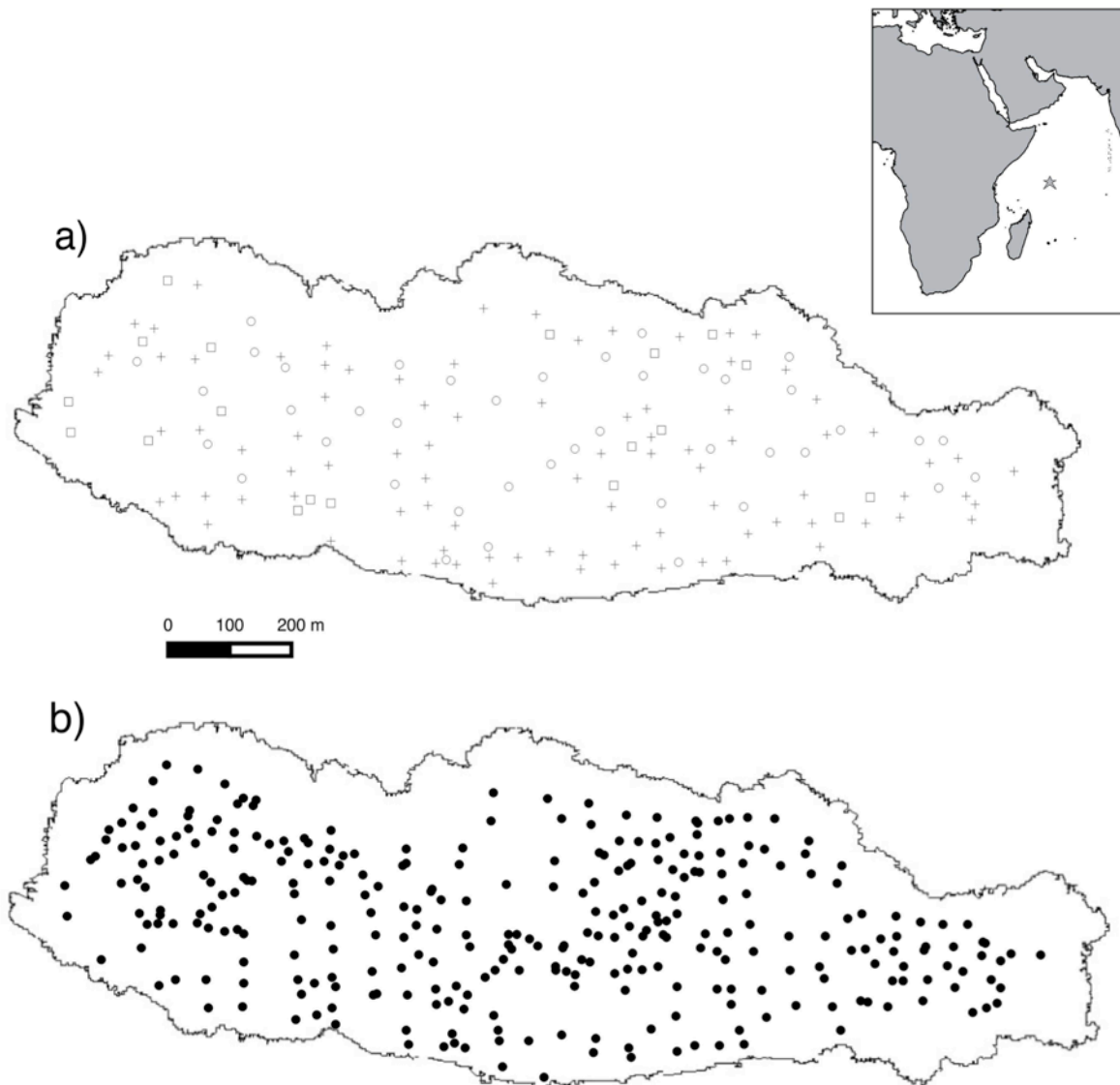


Figure 3.1. a) Map showing the plots surveyed in 2012 (\square), added in 2013 (o) and 2014 (+).
b) Map showing the 303 habitat survey plots. The star indicates the position of Aride Island in the Indian Ocean.

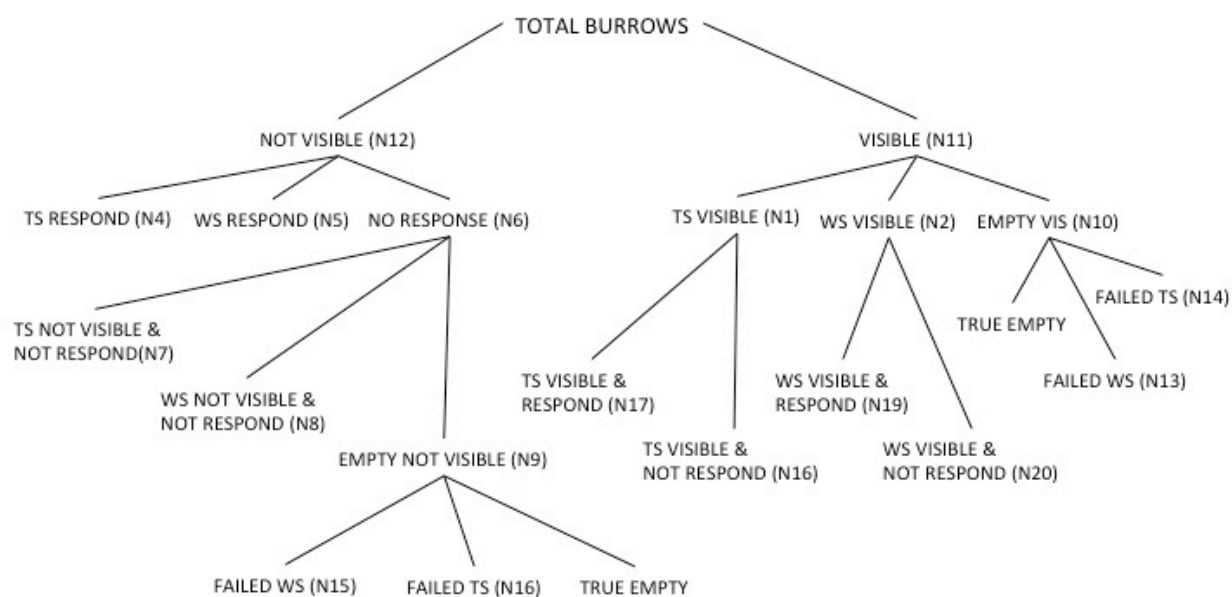


Figure 3.2. Possible options for the content of a burrow depending whether it is visible or not, and whether birds respond or not to the playback.

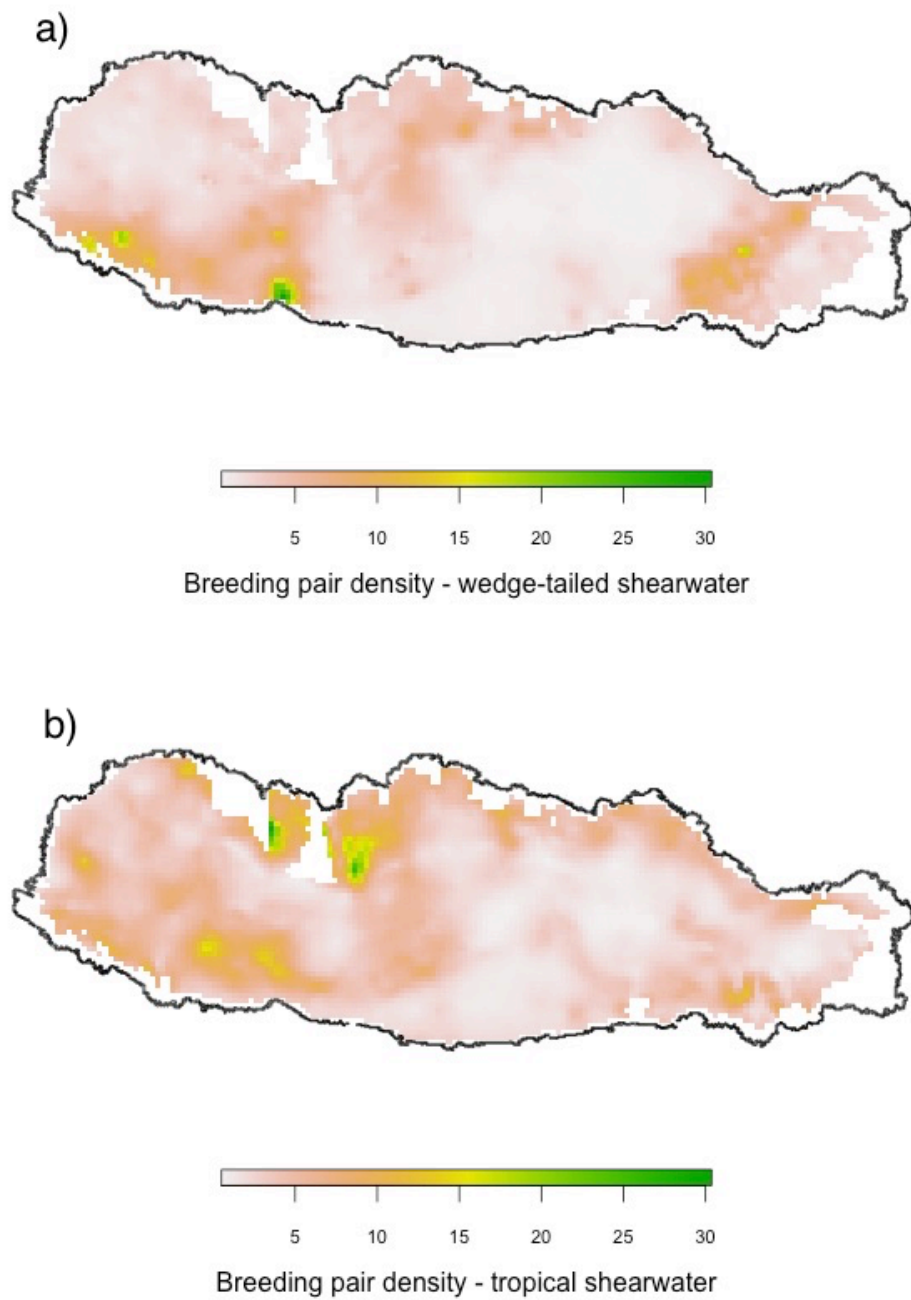
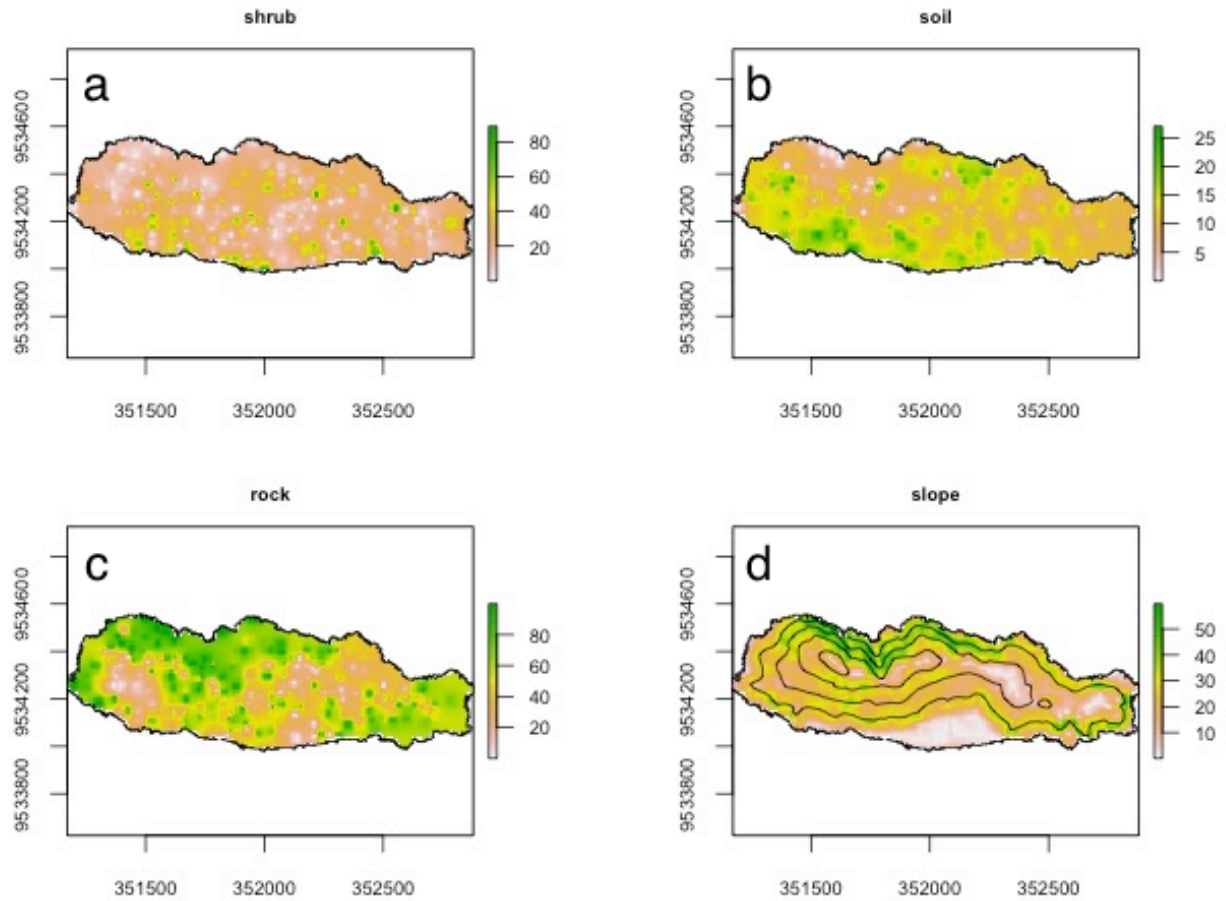


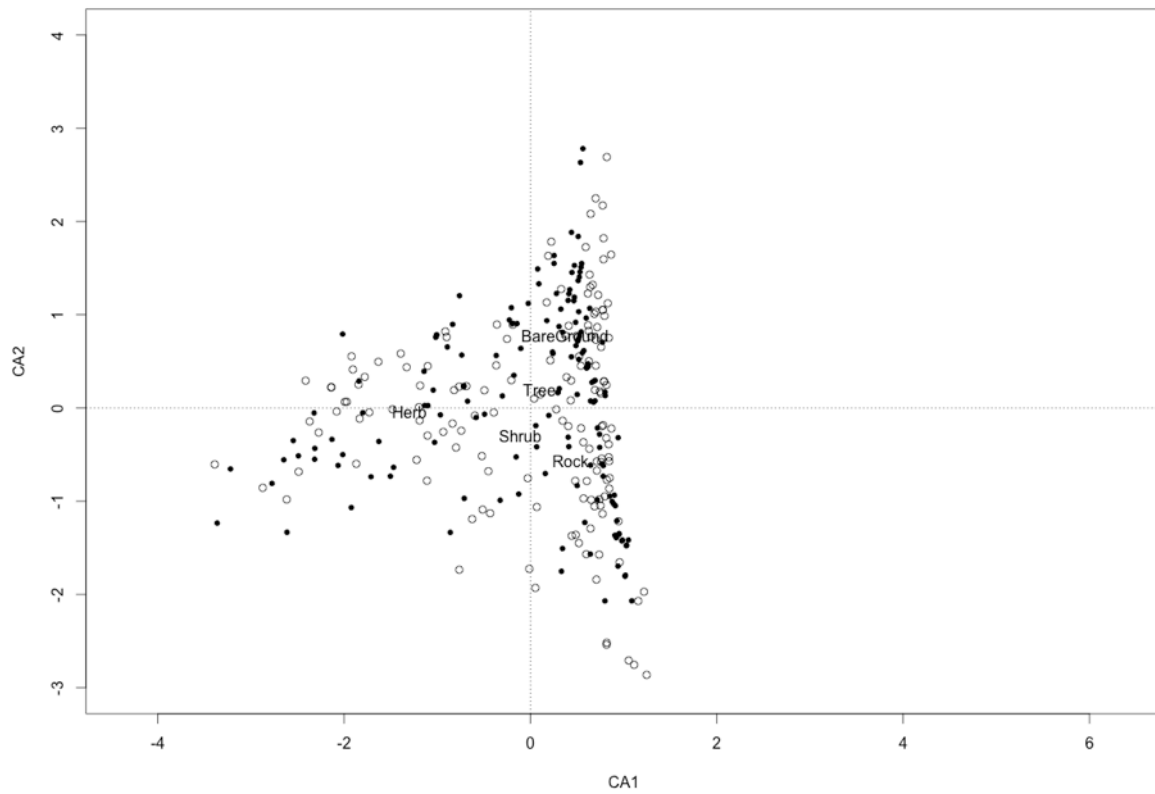
Figure 3.3. Predictive habitat model of the abundance and distribution of wedge-tailed (a) and tropical (b) shearwater breeding pairs on Aride Island in 2013-2014.

Appendixes

Appendix A. Distribution of the different habitat features across the island. (a) Shrub cover, (b) soil depth (c) rock cover and (d) slope with altitude isoclines every 30m.



Appendix B. Distribution of the 150 selected plots (•) and of the 303 habitat plots (o) based on habitat features (principal component analysis).



Appendix C. Logical steps for the calculation of the number of breeding pairs per plot accounting for response rate and breeding success.

The following procedure shows how to calculate the number of pairs per plot accounting for imperfect detection, breeding failures and coexistence of the two species.

Figure 3.2 reported in the text shows all the options could be addressed to a burrow considering the presence of both tropical (TS) and wedge-tailed shearwater (WS). We use the data collected during the shearwater census 2011-12, 2012-13 and 2013-14.

The assumptions are:

- The response rate for both species doesn't vary in space and among seasons but vary in time within the breeding season.
- The proportion of occupied burrows (per each species) on the total can vary with space but not among seasons.
- A burrow is occupied by only one pair that can be either TS or WS.

The total number of pairs per plot (see full text for further details), can be calculated as:

$$\text{TOT WS} = N2 + N5 + N13 + N8 + N15 \quad (1)$$

$$\text{TOT TS} = N1 + N4 + N14 + N7 + N16 \quad (2)$$

Where N1 and N2 are the number of visible TS and WS, N4 and N5 the number of TS and WS that were not visible but responded to the play-back. N14 and N13 are the portion of empty nests which are empty due to failures, N7 and N8 are the number of pairs present but not detected while N16 and N15 are the portion of undetected empty which are empty due to failure respectively for TS and WS.

N1, N2, N4 and N5 are available from the data. Below we show how to calculate the non-observable terms.

1. Estimation of failed nests for both species (N13 and N14)

To estimate the number of burrows not detected as occupied because of premature failure of the breeders we used all the detected nests (both empty and occupied) per plot during the three seasons and we calculated the proportion of occupied burrows (for both WS and TS) and empty burrows per each month as indicated below.

$$PWS_t = \sum N2 / \sum N11 \quad (3)$$

$$PTS_t = \sum N1 / \sum N11 \quad (4)$$

$$PE_t = \sum N11 - PWS_t - PTS_t \quad (5)$$

Where PWS_t and PTS_t are the proportions of occupied burrows for WS and TS respectively over the total of counted burrows at time t .

Figure C.2 shows the proportion of the empty or occupied burrows as calculated by (3), (4) and (5) monthly. The decrement of WS proportion in time is predictable due to breeding failures and end of the breeding season.

As the occupancy proportion can be variable within space and time and we want to estimate how many burrows detected empty were occupied at the beginning of the breeding season we consider the plots surveyed at month = 1 (November) during the

three surveys and we calculate the average proportion per each of them (Figure C.3). Once assessed the burrows occupancy proportions per each of the 73 plots surveyed at month 1 (and any of the three seasons) the inverse distance weighting interpolation was applied to obtain a occupancy proportion for both WS, TS and empty burrows for the whole island at 1 hectare resolution (Figure C.3) which are indicated as Pws_t, Pts_t, Pe_t . Where $t = 1$. N13 and N14 can be calculated for the plots being surveyed after November as:

$$N13 = N10 * Pws_t$$

$$N14 = N10 * Pts_t$$

2. Estimation of pairs present but not detected as not seen and not heard (N8, N7 and N9)

If the number of unknown burrows (see text for better explanation) for which no answer was heard (N6) is smaller or equal than the total of unknown burrows. N6 can be split between:

N8 = WS present but not visible and not responding

N7 = TS present but not visible and not responding

N9 = empty burrow

In turn N9 can be split in:

N15 = burrows empty due to premature WS breeding failure (occupied by WS at the beginning of the season)

N16 = burrows empty due to premature TS breeding failure.

Per each Julian date the response rate of both species was calculated combining the three census data (Figure C.1). Considering that the breeding season of WS starts normally in October, the 1st of October was taken to be Julian date = 1. The response rate was calculated as:

$$RTSi = N17i / N1i$$

$$RWSi = N19i / N2i$$

Where RTSi and RWSi are the response rate for TS and WS respectively at time (Julian date) i. Figure C.1 shows the response rate trend and the relative linear equations, which are:

$$yW = -0,0029x + 0,8647$$

$$yT = 0,0002x + 0,6283$$

Where yW and yT are the WS and TS response rates respectively, based on x, which represents the date.

If x is the date a single plot was surveyed then it is possible to calculate the response rate per each plot based on the linear trend.

If N4+N7 is the total number of not visible TS that were tested with the playback then N4+N7 multiplied by 1-response rate is the number of TS not visible that didn't reply (N7). The same logic can be applied to the WS. Therefore:

If

$$(N5+N8)*(1-yW) = N8 \quad \text{and} \quad (N4+N7)*(1-yT) = N7$$

Then

$$N8 = N5 [(1-yW)/yW]$$

$$N7 = N4 [(1-yT)/yT]$$

$$N9 = N6 - N8 - N7$$

3. Estimation of failed nests within the unknown burrows (N15 and N16)

As we considered failures (N13 and N14) within the visible and empty burrows (N10), now failures need to be considered within the estimated empty ones (N9). We apply the same rule applied for N10 using the species and empties proportions calculated in (3) and (4).

$$N15 = N9 * P_{ws_t}$$

$$N16 = N9 * P_{ts_t}$$

Now we can calculate the number of pairs per plot accounting for breeding failure and imperfect detection.

$$TOT\ WS = N2 + N5 + N13 + N8 + N15$$

$$TOT\ TS = N1 + N4 + N14 + N7 + N16$$

To test the reliability of the formula the calculation was applied to the wedge-tailed February and May data of 2012 and 2013 seasons and the results compared with the respective November counts. As the formula should account for breeding failures across the season we expected the numbers of pairs calculated in February and May to be very similar to the numbers found in November. The Pearson correlation coefficient r^2 for the 2012 comparison November versus February was 0.6 and November versus May was 0.7 while for 2013 it was 0.7 and 0.4 respectively. Therefore, when more data are available (2013) the further we move from the laying period and the higher the error in accounting for breeding failures becomes, at least for the season 2013.

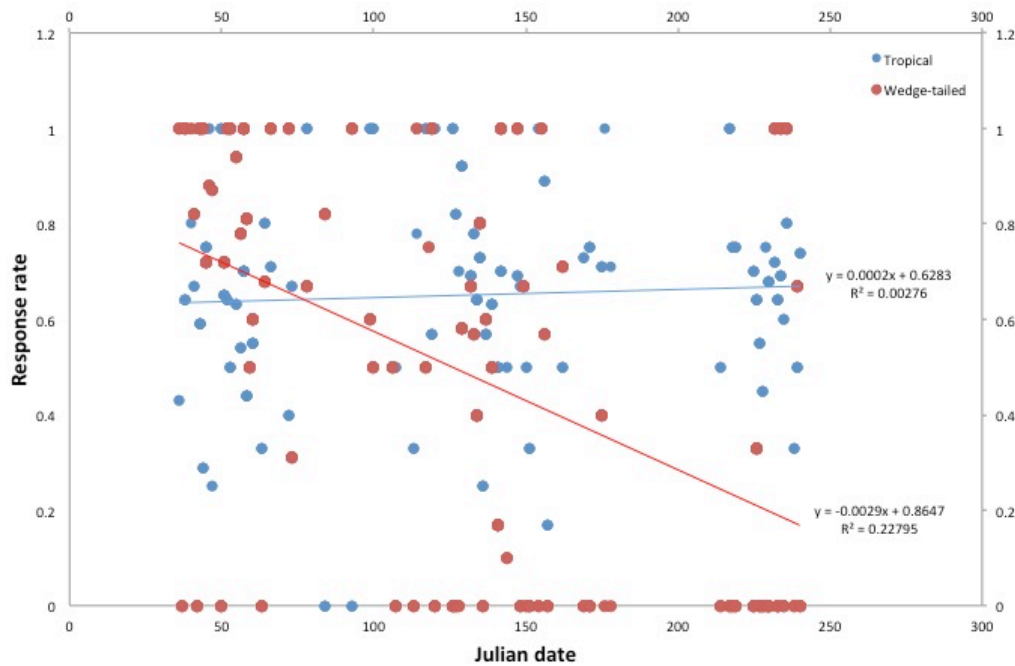


Figure C.1. Response rate trends from November to May. The red dots are the wedge-tailed response rate and the red line is the linear trend, which is negatively correlated with date. The blue dots indicate the TS response rate and the blue line the linear trend. The response rate results to be more constant for the TS throughout the whole season and doesn't show any particular trend. This can be supported by the fact that the species is all-year-round breeder. The response rate trend (red for wedge-tailed and blue for tropical) equations are also shown.

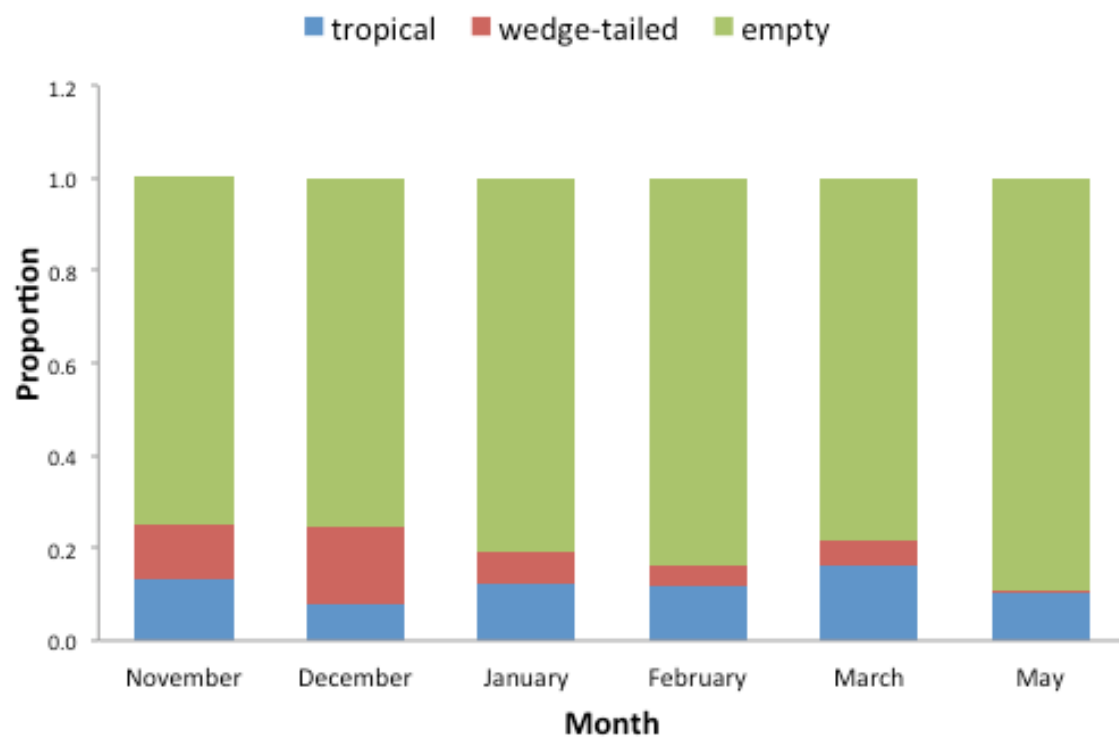


Figure C.2. Proportion of burrows occupied by the two species and empty during the period from November to May. April is excluded, as there were no surveys during this month.

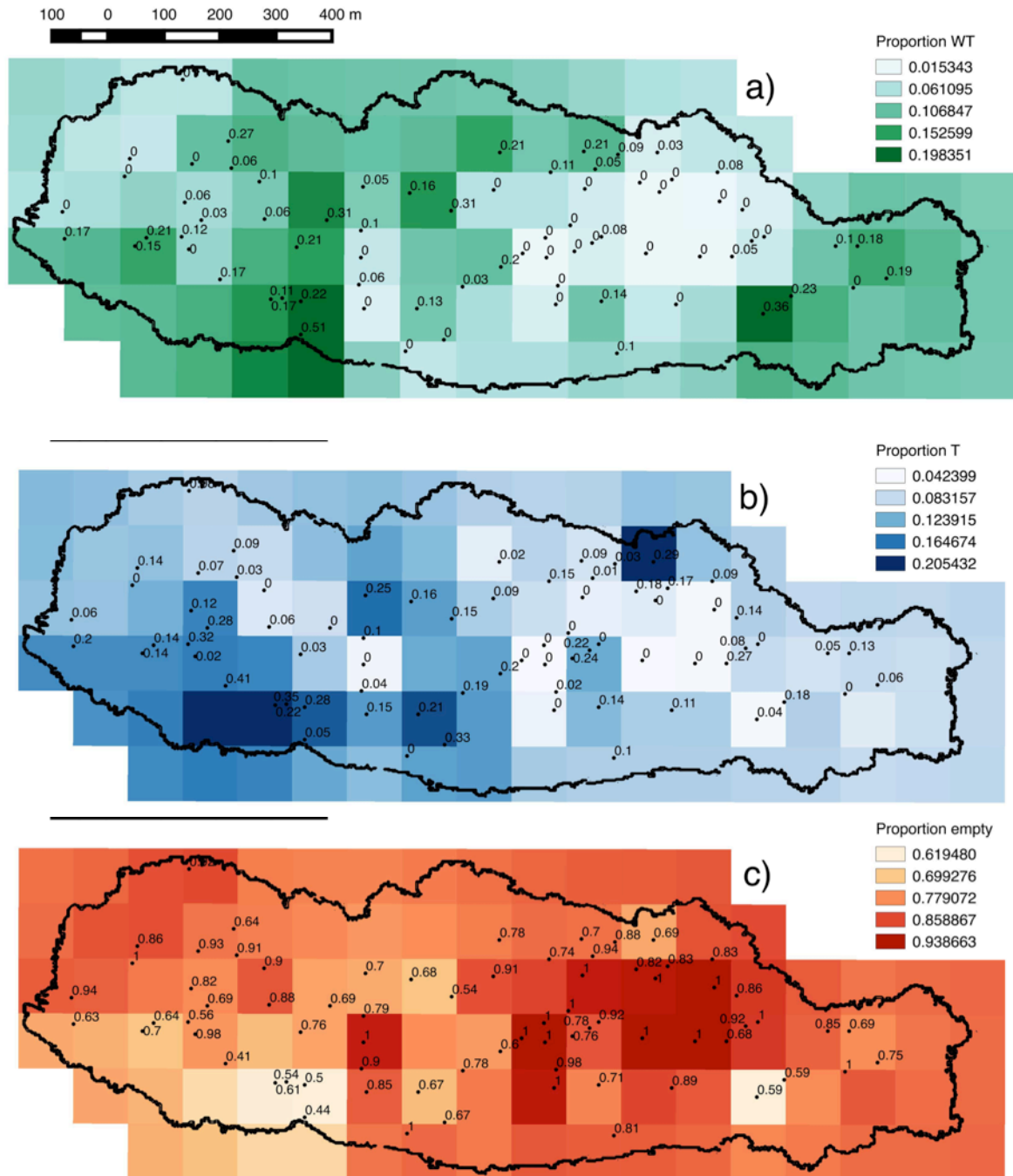
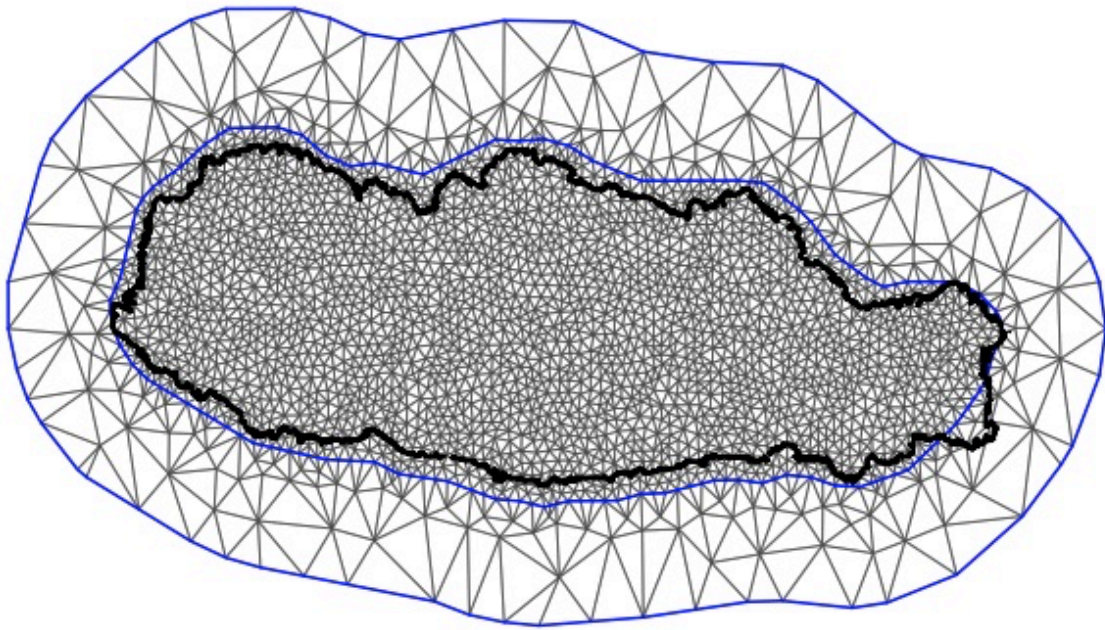


Figure C.3. Maps showing the proportion of wedge-tailed (a), tropical (b) shearwaters and empty (c) burrows interpolated at 1-hectare square. The values used for the IDW interpolation are indicated by dots and correspond to the average proportion of wedge-tailed, tropical and empty burrows found at each plot surveyed at least once during the first month of the survey (November).

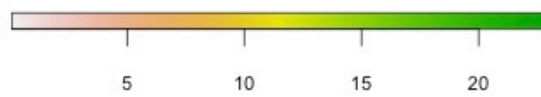
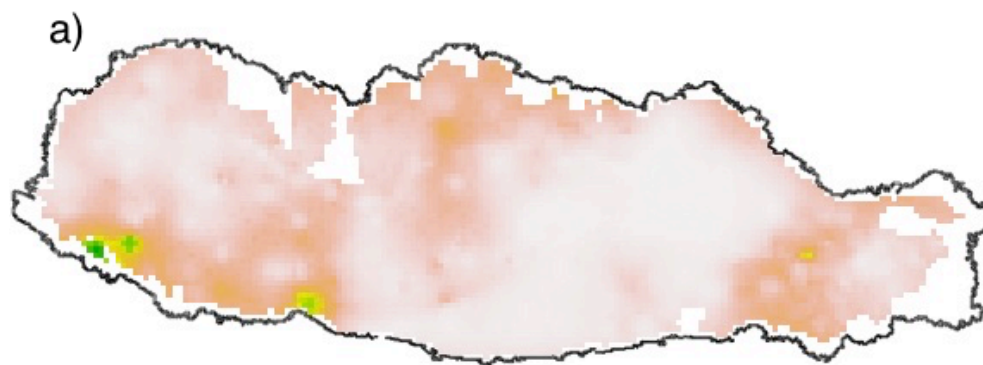
Appendix D. Model selection for the two pairs estimation methods (Method1 = Bayesian calculation, Method 2 = formula) indicating the AIC values, the delta AIC and the Akaike weights

Method 1				
Number	Wedge-tailed Shearwater	AIC	Δi	ωi
1	Shrub+ Rock+ slope+ slope^2+soil+jul	439.6	0	0.40
2	Shrub+ Rock+ slope+soil+jul	440.5	0.95	0.28
3	Shrub+ Rock+ Altitude+ slope+ slope^2+soil+jul	440.6	0.11	0.21
4	Tree+Shrub+ Rock+ Altitude+ slope+ slope^2+soil+jul	442.1	1.49	0.08
5	Tree+Shrub+ Rock+ Herb+ Altitude+ slope+ slope^2+soil+jul	444.0	1.86	0.03
Tropical Shearwater				
6	Shrub+slope	586.1	0	0.44
7	Shrub+ Altitude+ slope	587.0	0.83	0.27
8	Shrub+ Altitude+ slope+ soil	587.7	0.72	0.17
9	Shrub+ Rock+Altitude+ slope+ soil	589.2	1.48	0.07
10	Shrub+ Rock+Altitude+ slope+ soil+jul	590.6	1.47	0.03
11	Tree+Shrub+ Rock+Altitude+ slope+ soil+jul	592.5	1.87	0.01
12	Tree+Shrub+ Rock+Altitude+ slope+ slope^2+soil+jul	594.5	1.99	0.00
13	Tree+Shrub+ Rock+ Herb+ Altitude+ slope+ slope^2+soil+jul	596.5	2.00	0.00
Method 2				
	Wedge-tailed Shearwater	AIC	Δi	ωi
14	Shrub+ Rock+ Altitude+ slope+ slope^2+soil	608.7	0	0.37
15	Shrub+ Rock+ slope+ slope^2+soil	608.9	0.25	0.37
16	Shrub+ Rock+ Herb+ Altitude+ slope+ slope^2+soil	609.6	0.74	0.20
17	Tree+Shrub+ Rock+ Herb+ Altitude+ slope+ slope^2+soil	611.5	2.55	0.07
Tropical Shearwater				
18	Shrub+ slope	705.9	0	0.39
19	Shrub+ slope+soil	706.1	0.16	0.34
20	Shrub+ Altitude+ slope+soil	707.3	1.26	0.17
21	Shrub+ Rock+ Altitude+ slope+soil	708.9	1.56	0.07
22	Tree+Shrub+ Rock+ Altitude+ slope+soil	710.8	1.91	0.02
23	Tree+Shrub+ Rock+ Altitude+ slope+ slope^2+soil	712.8	1.97	0.01
24	Tree+Shrub+ Rock+ Herb+ Altitude+ slope+ slope^2+soil	714.8	2.00	0.00
Per each species and model, the table shows: AIC values, AIC differences Δi and Akaike weights				

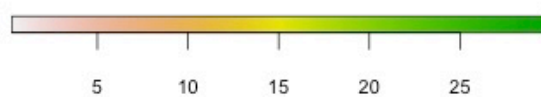
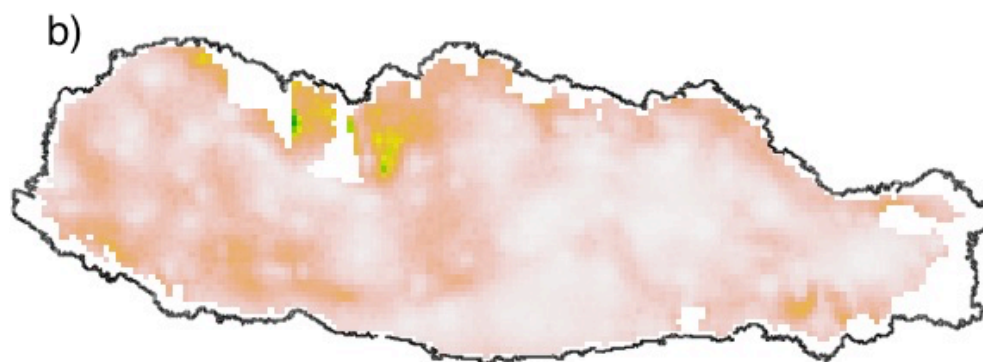
Appendix E. Constrained refined Delaunay triangulation.



Appendix F. Standard errors maps of the abundance calculation a) in wedge-tailed and in b) tropical shearwater.



Standard error - wedge-tailed shearwater



Standard error - tropical shearwater

CHAPTER 4

Comparative foraging distribution and ecology suggests interspecific competition between two sympatric shearwaters from the Seychelles

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Manuscript in preparation: Calabrese L., Pinaud D., Rocamora G., Bretagnolle V. (in prep.). Comparative foraging distribution and ecology suggests interspecific competition between two sympatric shearwaters from the Seychelles.

4.1 Introduction

Seabirds are particularly important indicators of the state of marine ecosystems (Furness and Camphuysen, 1997, Frederiksen et al. 2006, Zador et al. 2013), as they represent major predators of the oceans (Gaston 2004, Schreiber and Burger 2001). Seabirds are also amongst the most threatened birds globally and their decline has been documented in many geographical areas (Butchart et al., 2004; BirdLife, 2015). Threats are mainly related to habitat loss, introduction of predators, pollution, harvest and climate change (Grémillet and Boulinier 2009, Sydeman et al. 2012, Mills 2013). Whilst major menaces were first believed to be directed at the breeding colonies (and therefore, where most conservation actions were dedicated), increasing evidence acknowledges that threats at sea could lead to major declines (Furness 2002, Croxall et al. 2012,). Therefore, identifying foraging areas and habitat preferences at sea became a main focus for research and conservation (Lewison et al. 2012), in particular to assess any overlap between the distributions of birds and anthropogenic activities (Le Corre et al. 2012). This was made feasible by the development of telemetry technology (review in Wakefield et al. 2009). Such overlap may occur at any temporal stage (breeding or non-breeding) and spatial scale (localised, regional).

Long inaccessible for scientists, at sea distribution and foraging movements of small seabird species has become available over the past 20 years since devices for biologging have improved in terms of reduced weights and improved accuracy (e.g. González-Sólis et al. 2007, Phillips et al. 2007, Wakefield et al. 2009). However, studies on tropical seabird movements are still rather few when compared to research concerning their high latitude counterparts (Weimerskirch 2007), although some research has already been carried out in the tropical Indian and Pacific Oceans (Pinet et al. 2011, Le Corre et al. 2012, De Monte et al. 2012, Mannocci et al. 2014, McDuie, 2015) and in the Caribbeans (Jodice et al. unpublished). Resources in tropical seas are often less seasonal, less predictable and less abundant than in temperate and cold waters (Weimerskirch 2007). As a consequence, tropical seabird species are loosely associated to oceanographic characteristics (such as oceanographic fronts, eddies and upwelling) and their behaviour is not predictable; the exploited areas are often large and may vary in time depending on resources distribution.

In the tropical Indian Ocean, several hot spots have been identified at sea where different species gather in high densities, many of which are also targeted for human activities such as fishing, or for oil drilling (Rona 2003, Polacheck 2009). The seabird species in tropical areas seem to be strongly associated to sub-surface predators such as tuna and dolphins (Le Corre and Jaquemet 2004, Thiers et al. 2014); this association allows surface-feeding seabirds to forage on small fish brought up to the surface by the sub-surface predators. This relationship has been inferred for tropical terns, boobies, frigatebirds (Thiers et al. 2014) and also for the wedge-tailed shearwater (Balance et al., 1997; Catry et al. 2009b). Therefore, interspecific interactions may be a key component of habitat selection processes if resources are scarce and competitors numerous (Balance et al., 1997). In fact, competition has been recognized as one of the main forces driving population distributions and community dynamics (Dhondt 2012). Recently, the first ecological niche theory (Hutchinson 1957) was extended by Basille et al. (2008) and Calenge (2011) in order to incorporate habitat selection. In fact, the available habitat for a species can be represented as a volume described by different environment variables, within which habitats used by the species represent the ecological niche

(Basille et al 2008). Thus the comparison between different species habitat niches can be useful to assess eventual habitat selection overlap and to detect competition mechanisms among species sharing the same geographical areas (Rosenzweig 1991 & 1974, Hirzel et al. 2002, Morris 2003, Thuiller et al. 2013).

In this study, we focused on spatial (including depth) and temporal segregation between two sympatric species of shearwaters breeding in the tropical Indian Ocean, the tropical (*Puffinus bailloni*) and the wedge-tailed shearwater (*P. pacificus*). Interspecific competition between these two species is expected to occur, since both breed in very high numbers in the same Seychelles islands (Calabrese et al. in review), and their diet largely overlaps in the area (Morisita-Horn overlap index = 0.8 in Catry et al. 2009a) as they both forage mainly upon Mullidae and Carangidae. However, the wedge-tailed shearwater also forages on cephalopods and the tropical shearwater on Engraulidae (Catry et al. 2009a). To our knowledge, there are no telemetry studies on movement at sea on the tropical shearwater while for the wedge-tailed a few studies have been carried out both in the Pacific (McDuie et al. 2015) and in the Indian Ocean (Catry et al. 2009b, Cecere et al. 2013). For both species, our first aim is to describe foraging areas exploited during non-breeding as well as breeding seasons (mainly late chick rearing); second, we aim to assess variation between years and monsoon seasons, and to derive habitat suitability maps. Third, we investigate possible habitat segregation resulting from competition between the two species by analysing spatial, depth, and temporal overlaps (at different periods).

4.2 Materials and methods

Study species and locality

Our study was carried out on Aride (4° 12' 46"S, 55° 39' 53"E), a rat-free island declared nature reserve in 1975 (Warman and Todd, 1984). Aride is part of the Seychelles archipelago and hosts one of the largest seabird population of the western Indian Ocean, which includes ten species of breeding seabirds. It is an Important Bird Area (Rocamora and Skerrett 2001) and it hosts about 30,000 and 15,000 pairs of tropical and wedge-tailed shearwaters respectively (Calabrese et al. in review).

The tropical shearwater (TS) is widespread in the tropical Pacific and Indian oceans (Austin et al. 2004). Its main known breeding colonies are situated in the Seychelles and Phoenix archipelagos (Calabrese et al. in review). In the Seychelles, TS breeds all year round, but with three main peaks of egg laying in April, July and November (see APPENDIX I). Aride is its largest known colony of the Indian Ocean and possibly of the world (Calabrese et al. in review). The TS is the only small shearwater breeding in the Malagasy region (Safford and Hawkins 2013) though it is represented by no less than five subspecies (Bretagnolle et al. 2000), some being perhaps better considered as species (e.g. *persicus* and *temptator*). The movements at sea of this species are poorly known. It is considered an intermediate-distance forager confined within 80-300 km from breeding sites (Safford and Hawkins 2013). Immature individuals could be more dispersive than the adults and the species could reach the Indian continent including Sri Lanka (Praveen et al. 2013). It is often associated with schools of tuna and it is often mixed in feeding flocks with other species such as brown noddy (*Anous stolidus*) and other local breeding birds (Jouanin 1987, Shirihihi & Bretagnolle 2015).

This species is believed, as with many other petrels, to display a post-breeding pre-basic moult (Marchant and Higgins 1990).

The wedge-tailed shearwater (WTS) range includes the Indian and Pacific oceans at tropical and subtropical latitudes. In the granitic Seychelles, the main colony is found on Cousine Island with tens of thousands of pairs (Skerrett et al. 2001) and the breeding season lasts from October/November to February/March, even if few pairs can be found breeding year round (see APPENDIX I). The other large colony in the Seychelles can be found on St Joseph Atoll, in the Amirantes archipelago (Kappes et al. 2013). Its movement at sea have already been documented for the Indian Ocean (Catry et al. 2009b) during inter-breeding and chick rearing periods, and for the Pacific and Indian Ocean during the breeding season (Week et al. 2013, McDuie et al. 2015, Cecere et al. 2013). WTS appears to be mainly pelagic, preferring deep and poor waters rather than rich continental shelves areas (Catry et al. 2009b, Baley, 1968). However, it is often associated to oceanographic features such as eddies or upwelling (Week et al. 2013, Cecere et al. 2013) and to sub-surface predators like tuna and dolphins (Balance et al. 1997; Catry 2009b). WTS also shows adult post-breeding pre-basic outwards moult (Marchant and Higgins 1990).

Monitoring devices

Geolocators are telemetry devices with light weight and a long lasting lifespan, thus allowing monitoring small birds during long periods (Phillips et al. 2004, Bridge et al. 2011). They record light intensity, Global Mean Time (GMT) and wet/dry state of the device. Some of them can also measure the temperature when submerged (Gaston et al. 2011, Thiebot and Pinaud 2010). The individual positions are assessed only when (and if) the device has been retrieved and the data downloaded. The geolocation theory uses the time midway between dawn and dusk and the local apparent noon to determine the longitude, while the day length is used to determine the latitude (Hill, 1994), based on the fact that each place on earth has different time of sunrise and sunset and different day length (Hill, 1994). The accuracy in determining the different locations has been assessed at 186 (\pm 114) km (Phillips et al. 2004) and 202 (\pm 171) km (Shaffer et al. 2005), and it can be influenced by shading due to weather and individuals' habitats and behaviour (such as topography and woodlands), or alteration of records due to artificial lights (Thiebot and Pinaud 2010, Lisowski et al. 2012). The error in the estimate for latitude is smallest during times and for places where day length strongly varies with latitude (Hill 1994), therefore it becomes very high around the two equinoxes when day length is similar all around the globe (Hill 1994; Ekstrom 2004) and near the equator where there is little variation in day length (Lisowski et al. 2012). Conversely, the longitude estimation is equally accurate all year round at all latitudes except the ones where at certain periods of the year the sun never sets (Hill, 1994). To improve latitude estimations, especially in periods close to the equinox, a calibration can be performed before and after the device deployment. It consists on leaving the device in conditions similar to the conditions the animal will experience when it will be equipped with it. It can be directly attached on the animal, "in-habitat calibration" (if its presence on a given place is sure), or fixed in an open area with a clear view of the horizon, "roof-top calibration". The calibration have to last at least 5-7 days and it accounts, to some extent, for systematic deviations in day/night length improving the latitude estimation by matching the correct sun elevation angle to the chosen light (Lisowski et al 2012,

Thiebot and Pinaud 2010). For this study we carried out the “roof-top calibration” for an average of 10 days before and after devices deployment.

Fieldwork was carried out between June 2012 and June 2014. During this period a total of 54 geolocators were deployed on TS and 57 on WTS. All the geolocators were deployed on breeding adults with large chicks, either fully feathered or showing a mix of down and feathers (towards the end of the breeding season). The geolocators on TS were deployed during three main periods: August 2012, June 2013 and April/June 2014. On WTS they were deployed at the end of the two breeding seasons 2012-2013 and 2013-2014, in February/March. Thirty-eight Mk4083 geolocators (provided by Biotrack Ltd.) measuring $17 \times 10 \times 6.5$ mm and weighing 1.9 g (1.06% of the mean adult mass measured during this study: 179 ± 18 g) and 16 Intigeo C65 (Migrate technology) measuring $14 \times 8 \times 6$ mm (0.55% of mean adult mass) were deployed on TS. All the 57 geolocators deployed on WTS were Mk3005 (Biotrack Ltd.) measuring $16 \times 14 \times 6$ mm and weighing 2.5 g (0.73% of the mean adult mass measured during this study: 343 ± 39 g).

Each logger was attached to a metal ring on the tarsus using 1 or 2 UV resistant cable ties. The total weight of the devices plus the ring and cable ties were 1.6 and 1.0% body mass of TS and 1.0% body mass of WTS. All geocator models measured light levels every 60 s, of which the maximum value is sampled every 5 minutes. All tracked birds were blood sampled from the tarsal vein at their return to the colony when the device was removed, or before it was deployed. The sex was assessed using molecular methods (Fridolfsson & Ellegren 1999) with the DNeasy Blood & Tissue Kit. The light data obtained by the geolocators after retrieving were analysed using a combination between the GeoLight and tripEstimation packages (Thiebot and Pinaud 2010), developed within the R software framework (Sumner et al. 2009, Sumner and Wotherspoon 2015, Lisovski and Hahn 2013, R Development Core team 2015). This method allows constraining the locations calculation by a land mask, the start and end points of the trajectory (usually the colony) and the average bird's speed within 12 hours. The locations coordinates were calculated using a state-space model using a Kalman filter (Kalman 1960). We used the following model parameters: the colony was taken as start and end point (except when the device did not record the whole trip), the average speed over 12 hours period was set at 30 km/h (with a variance of 15 km/h) for TS and at 35 km/h (20 km/h) for the WTS. Average speed settings were set based on literature on similar or the same species (Catry et al. 2009b, Pinet et al. 2011, Cecere et al. 2012). The model was then implemented using simulations and MCMC (tripEstimation package) to improve the spatial likelihood of the tracks. The calculation provided two most probable locations per day, one at sunrise and one at sunset. Using this method, the estimation of locations during equinox periods is made possible therefore the whole trips were used for the data analysis.

The geocator salt-water sensor allows detecting when a bird is on the water, while the light data allows assessing if the bird spends the day at the colony in its burrow. In addition, to record the shearwaters diving depth, 10 Archival tags (3 LAT2900 and 7 LAT1900) were deployed from June to August 2012 on 30 TS during the early chick-rearing period. During the breeding season 2013-2014 (from December 2013 to March 2014) an additional 10 Archival tags (LAT 2900) were deployed on 24 WTS during early chick rearing. The devices were attached to the leg with a plastic ring and a cable-tie. The archival tags LAT1900 and LAT2900 measured $8 \times 15 \times 7$ mm and weighted 2.0 g (1.06% of the mean adult mass of the tropical shearwater, see above for details) while

the LAT2900x deployed on WTS measured 11 x 15 x 9 mm (1,0% of mean adult mass measured during this study, see above).

The devices were deployed at night (after the adult had fed the chick), they were left for one day and then removed the consecutive night or as soon as the bird was found again in the colony. The nests were visited every three hours from 19:00 PM to 4:00 AM in order to increase the chance of re-capturing the birds with the devices. All archival tag data were analysed with the program LAT Viewer Studio 2.10.8 (Lotek 2014).

Statistical analyses

To carry out the data analysis, and given the fact that we generally lacked data for late incubation period and early chick rearing (see Table 4.1 for details), we considered three main periods: late chick-rearing, non-breeding (i.e., between two breeding attempts), and early breeding (called pre-breeding further in the text), which encompass mating, pre-laying exodus, and early incubation. The chick-rearing period was assessed using the visual analysis of the trajectories, combined with nest checks at the colony. It ended when the trajectory of the birds started to leave the colony area (buffer of about 500 km) towards wintering areas, then the start time of the migration was set. For some birds, it was difficult to assess the beginning of the migration, therefore only nest monitoring data were used. After the non-breeding period, the birds normally come back to the colony to meet their partners and defend their burrows. We assessed the end of the way-back migration (and end of non-breeding period) using both activity and light data. We consider the migration to be over when the first visit at the colony was made to occupy the burrows, i. e. when the light sensor did not detect light during the day and/or when the wet/dry sensor was dry during all night. The pre-breeding period was considered from the first visit to the colony after the return migration until when the device was retrieved. The location of birds in the three different periods were analysed combining or separating years (for the WTS), or the monsoon seasons (for the TS), to detect potential season effect. In fact, the tropical Indian Ocean weather is dominated by the monsoons trade winds. From October to March the wind is weak and comes prevalently from North-West (North-West monsoon season), while from April to September the wind gets stronger and blows mainly from South-East (South-East monsoon season) (Stoddart 1984). These two monsoon seasons will be used for the analysis.

For each period, a kernel analysis was performed using the R package “adehabitatHR” (Calenge 2015). The 50% density contours represented the activity core area while the area of active use was set within the 95% kernel contours (see Hamer et al. 2007, Catry et al. 2009b, Pinet et al. 2011). Within each period, differences among sexes and years were assessed using the proportional overlap of the 50 and 95% kernels (González-Solís et al. 2000, Hyrenbach et al. 2002). The TS breeds all year round in Seychelles, therefore the difference between birds distribution between the two monsoon periods (North-West and South-East, from now on called NW and SE respectively) was assessed for non-breeding and pre-breeding periods. We could not compare chick-rearing distribution patterns between the two seasons as only the SE monsoon was represented in the data. For the WTS, we compared the differences among years for all three periods.

Then, we sought for species preferences in terms of marine habitat by using the ecological-niche factor analysis (ENFA). ENFA is based on the concept of ecological niche (Hutchinson, 1957), and provides a suitable way to analyse presence-only data. It is a

multivariate technique that is mainly used for explorative purposes and in particular for building habitat suitability maps (Basille et al. 2008). ENFA also allows identifying the habitat features that are preferred by the population of interest (Basille et al. 2008). Two parameters are extracted from the analysis, marginality and specialization. The former is the distance between the centroid of the selected (or used) habitat and the origin of the ecological space that describes the available habitat. The higher the marginality, the higher the difference between average available habitat and average selected habitat will be. Specialization is a measure of niche breadth, more an animal (or population, species) will choose a narrow range habitat and the higher this measure will be. ENFA also provides a measure of the weights that single habitat variables have on marginality and specialization. ENFA was performed with the R package *adehabitatHR* (Calenge, 2011), which further allows a visual representation of available and used habitat. Habitat suitability maps were based here on Mahalanobis distances as obtained with Factor Analysis (MADIFA), in the form of probability of occurrence maps (i.e. the probability to find a given species in a certain area based on the habitat features).

For both ENFA and MADIFA analyses we selected environmental variables that were suspected to play a role in shearwaters' distribution at sea, based on bibliographic information of the species foraging behaviour (Catry et al. 2009b, Cecere et al. 2013, Week et al. 2013). The marine ecosystem was thus characterized by bathymetry (m), slope (degrees), sea surface temperature (SST, °C), wind speed (m/s), chlorophyll *a* concentration (mg/m³), and total tuna catch (MT). The bathymetry was obtained from the NOAA's ETOPO 1 minute data-set, the slope was derived from the bathymetry using four neighbouring cells (package *raster* in R software). The SST and the wind speed monthly average data were downloaded from the database BloomWatch 180 (<http://coastwatch.pfel.noaa.gov>). The chlorophyll *a* was obtained from the NASA earth observation database based on AQUA/MODIS at one-month resolution data (<http://neo.sci.gsfc.nasa.gov>) and was used as an indication of primary production in the upper layer of the ocean. The tuna total catch was derived by data on purse seine fishery in the Indian Ocean through information made available from the Indian Ocean Tuna Committee (IOTC, <http://www.iotc.org/data/datasets>). Tuna catches were used as a proxy of the distribution and abundance of tuna in the Indian Ocean. All the environmental variables were reshaped at 1 degree resolution grid, to account for the location error given by the geolocation. The study area was delimited by latitude (+ 30°, - 30°) and longitude (+30°, +105°) where both species could be potentially found. For the chick-rearing period, the latitude and longitude delimiting the study area were set at -20°, +10° and + 30°, + 70° respectively.

4.3 Results

Devices recovery rate

We retrieved 31 and 40 devices out of the 54 and 57 deployed on TS and WTS respectively. For the TS, the general recovery success was 57% while for WTS it was 79% for the breeding season 2012-13 and 53% for the season 2013-14.

However, due to manufacture failure on entire series of devices (only for Mk 4083 and Mk 3005), 12 (TS) and 25 (WTS) devices failed to download any data and we could only recover a very small proportion of them (despite being sent to the manufacturer for data extraction). For subsequent analyses, only trips of a duration superior of two weeks

were kept, i.e. 10 trips (2013) and 7 trips (2014) for WTS and 26 for TS (see Table 4.1 for all details). Figure 4.1 shows the trips' temporal distribution throughout the study period. Table 4.1 shows the average duration of chick rearing, non-breeding and pre-breeding periods recorded during this study and the respective maximum distances travelled by each tracked bird. The average (\pm SD) non-breeding period was 176 (\pm 48, N=15) days for TS and 118 (\pm 20, N=15) days for WTS (considering only the trips where the non-breeding period is complete). The average (\pm SD) maximum distance travelled by the TS and WTS during such periods was 1757 (\pm 747) and 3618 (\pm 716) km respectively.

Loggers had no apparent impact on WTS, as it was already found by Catry et al. (2009b). All chicks of the equipped birds during the years 2012 and 2013 fledged successfully for both WTS and TS. The only visible effect on the TS was the presence of a small callosity at the lower tarsus extremity, noted on 60% of birds for which the GLS were recovered. High recovery rates for both WTS and TS were expected given adult survival rates of very similar species which is a minimum of 0.95 for Christmas (*Puffinus nativitatis*), sooty (*P. griseus*) and flesh-fooed (*P. carneipes*) shearwater (species very similar to WTS; Mougin 1999) and 0.82 for Audubon shearwater (*P. lherminieri*) (sister species of TS; Precheur et al. in review), and accounting for sabbatical years in shearwaters (up to 20%: Mougin et al. 2002).

Overlap analysis

For WTS the 95 and 50% density contours areas exploited during late chick-rearing period (Figure 4.2) in 2013 and 2014 overlapped by, on average, 69% and 40% respectively, whilst non breeding areas overlapped by 84% and 45%. However, there were some differences in the pre-breeding period, where the density contour area in 2014 was much larger (but included the ones exploited in 2013), with a mere 20% and 30% of overlap (for 95 and 50% kernel respectively). Despite some differences, we merged both years for all three periods (including pre-breeding, since the 2013 area was completely included within the 2014 one). For the TS (Figure 4.3) we considered the two monsoon periods except for chick-rearing since only SE monsoon data were available. In contrast to WTS, we found poor overlap among non-breeding areas with an average overlap of 39% and 35%, while for pre-breeding periods the overlap was 57% and 65% (but there are only 2 individuals representing the SE monsoon period for the pre-breeding).

Habitat selection

The average oceanographic characteristics in the kernel of late chick-rearing, non-breeding and pre-breeding distributions of TS and WTS are provided in Table 4.2. The MADIFA and ENFA analysis were performed for both species on normalized habitat variables. For the WTS, the non-breeding period showed a preference for deep and open waters (i.e. low values of bathymetry - negative values were used), away from coastlines or upwelling systems and ridges (i.e., low values of slope selected). WTS did not select high values of chlorophyll but preferred areas with high SST, low wind speed and medium tuna catch (see Table 4.3 and ESM 4.1). In contrast, during the pre-breeding period, areas with mid-low bathymetry and high slope values were selected, with preference for middle values of wind and SST, mid-high values of chlorophyll and areas with high tuna catch (Table 4.3 and ESM 4.1). Marginality was higher in pre-breeding

areas than in non-breeding ones (Table 4.3), while specialization was 7 and 19 times narrower than the available ecological niche for non-breeding and pre-breeding periods respectively. During the non-breeding period, four variables were mostly selected, the SST, the tuna catch, the wind and the chlorophyll, with SST contributing most to marginality (coefficient = 0.64) followed by tuna catch (0.44) and wind (-0.42). The chlorophyll was important for the specialization axis (0.79). Based on the specialization, the birds were restricted to a limited range on this variable. During the late chick rearing, the adults remained close to the colony, around the Seychelles microcontinental platform and selected areas with low values of wind and high values of slope and tuna catch (see ESM 4.1).

For TS, given the poor overlap in their distributions during the NW and the SE monsoon seasons, chick-rearing, non-breeding and pre-breeding periods were analysed separately (see ESM 4.1 and Table 4.3). The results of both niche histograms (ESM 4.1) and ENFA of non-breeding and pre-breeding were comparable for both monsoon seasons. The TS showed a preference for low bathymetry and low wind speed, high tuna catch and high SST values and middle chlorophyll values (ESM 4.1 and Table 4.3). The only variable that differed between these two periods was slope, with higher values (shallow waters) during pre-breeding. The non-breeding and pre-breeding adults therefore choose deep and warm waters with low wind force and nor high or low chlorophyll concentration. They were also associated to areas with a high level of tuna catch. Marginality for both periods was driven by tuna catch, wind and SST (see Table 4.3). Specialization was also very high (40 for non-breeding and 120 for pre-breeding), and most affected by the variables SST and wind. During the SE monsoon period, the preferred habitat was very similar in non-breeding and pre-breeding areas, differing in bathymetry values (deep water for the former, shallow water for the latter). During pre-breeding, the TS selected shallow areas, while during non-breeding TS selected for low wind in NW, higher wind speed and slope values during SE. Moreover, during the pre-breeding, high and low values of bathymetry were preferred for the NW and SE respectively. Interestingly, despite the fact that areas exploited during the NW and SE monsoons by TS spatially differed, the habitat niche remained fairly constant between these two periods within seasons. Contrarily, the habitat features selected during late chick rearing during the SE were characterised by high values of slope, chlorophyll and tuna catch (see ESM 4.1).

Habitat suitability maps

Habitat suitability maps for both species obtained with the MADIFA analysis are presented in Figure 4.4 for WTS (with both years pooled) and in Figure 4.5 for TS (one map per period and per season). During the inter-breeding period, suitable areas for WTS included most of the tropical Indian Ocean basin, excluding coastal areas (see ESM 4.1). These areas reflect the WTS preference for deep-sea areas with low slope and wind, high SST and mid-low values of chlorophyll. During the pre-breeding period the suitable areas for the species (Figure 4.4) were much more localized around the colony.

The potentially favourable areas for the TS were much more localized than for the WTS. During the non-breeding period, in the SE monsoon season, they were concentrated around the Seychelles, in particular in the mascarene basin and between the Seychelles and the African east coast where the slope and tuna catch were high and the water not too warm (the highest temperatures were avoided during this period - see histogram in ESM 4.1). During the NW the most suitable areas extended towards the

north-east (Figure 4.5a, towards the Chagos archipelago) and the south-west (Comoros and Mozambique channel) with habitat features comparable to the ones selected during the SE monsoon. During the TS pre-breeding period for both the SE and NW seasons, the most suitable areas were restricted around Seychelles, therefore characterized by shallow waters, high tuna catch and low wind.

Diving depth

A total of 36 and 276 days of foraging activity were recorded during the chick rearing on 30 and 22 different TS and WT individuals, respectively. The maximum depth reached by the TS was about 16 meters and the average maximum depth was about 6.7 ± 4.1 m. Conversely, loggers deployed on WTS did not show any sign of significant deep diving activity. In fact, the maximum pressure recorded was -4 dBar. This pressure value can be associated to either a no-dive or a very shallow dive (between 1 and 4 m), therefore this species was behaving as a surface feeder.

4.4 Discussion

During the non-breeding period, both species preferred areas with high levels of tuna catch and low wind, with the WTS also selecting warm waters. There were only slight differences in habitat selection between the two species, and between monsoon seasons for TS, with only slope playing a role during the SE. Slope was indeed an important variable also during the pre-breeding period and chick rearing for both species (Table 4.3 and ESM 4.1), indicating the association of birds with upwelling zones. The fact that both species selected areas with high tuna catch could be an indicator that they are strongly associated with sub-surface predators, as also reported in literature (Le Corre and Jaquement 2004, Thiers et al. 2014, Piton and Magnier 1976). The triangle between Comores-Seychelles-Madagascar has been indeed identified as a particularly favourable area for tuna and other fish predators' abundance based on physio-chemical physico-chemical indices (Piton and Magnier 1976). During the non-breeding season, the WTS was already shown to forage in two main areas: between their colony and the Carlsberg ridge, and between the central basin and the Chagos archipelago (Catry et al. 2009). Here, we detected a third important site, around the Sri Lanka region, which was exploited by half of the tracked birds (7/15). This is concordant with regular observations off Sri Lanka, from May to September, where WTS is often sighted together with the flesh-footed shearwater (*Puffinus carneipes*, De Silva, 2011). This region is particularly rich in nutrients and it attracts many species of seabirds. In fact, the monsoon winds trade influences the Sri Lanka zone creating two important oceanic phenomena: the southwest monsoon (c. May–September), and northeast monsoon (c. November–March). In May the southwest monsoon causes upwelling of deep nutrient-rich water off the west coast of Sri Lanka; afterwards, the intensity of upwelling increases progressively off the western and southern coasts as the monsoon progresses. By July the upwelling increases greatly and encourages blooms of plankton, which enhance oceanic productivity providing ample nourishment for seabirds (such as boobies, tropicbirds and shearwaters) and other predators (De Silva, 2001). The TS has also been recorded a few times in the region (De Silva, 2001) but we found no evidence for such movements in our data, suggesting that these may just be sporadic events.

In habitat selection studies, the understanding of where a certain species can be found and why certain areas are selected is of fundamental importance (Rushton et al. 2004, Basille et al. 2008). From species preferences, important tools such as habitat suitability maps can be produced (Guisan and Zimmermann, 2000). Among tropical seabirds, information on habitat selection at sea and habitat suitability maps is often lacking. In particular, in the case of the tropical shearwater, the areas exploited during inter-breeding, pre-breeding and chick-rearing periods are described here for the first time. This species was believed to be an intermediate-distance forager (Safford and Hawkins 2013) but we found it migrating at a maximum of about 3600 Km from the breeding site (Table 4.1). The area including the Comoros Islands and the Somali basin seems to be the most exploited during the inter-breeding period in the NW monsoon season (Figure 4.3), while during the SE the movements of the TS are more limited to the areas surrounding the breeding colony, the mascarene basin and the East coast of Madagascar (Figure 4.3). The difference in distribution between the two different seasons can have multiple explanations.

First, as previously mentioned, the Indian Ocean region is influenced by monsoon trade winds. During the SE season (April-September) the strong southeast wind ascends the east coast of Africa (Fieux, 2001). This creates a strong Ekman transport from east to west (Price et al. 1987), which carries nutrients away from the coasts of Somalia, Arabia, India and Sri Lanka (Tomczak & Godfrey 2003) making the Seychelles surrounding waters more rich in nutrients than during the NW monsoon season. This allows the seabirds in the region to breed in high numbers (Skerrett et al. 2001, Rocamora & Skerrett 2001) and it could also attract the TS during the inter-breeding season, which does not have to move too far to find food.

Second, the breeding season of the WTS occurs during the NW monsoon season and both shearwater species share almost totally the same prey types (Catry et al. 2009b). Given that during the NW the waters surrounding the Seychelles plateau are poor in nutrients, the competition for resources could force the TS to leave the areas. In fact, the ecological niche of the TS is almost the same during both seasons but during the NW it covers a wider area. The competition for resources at sea with the WTS on the Seychelles plateau could force it to explore wider areas, resulting in spatial segregation. Spatial segregation can also be detected in the water column. During the early chick-rearing the WTS does not show any sign of diving activity, contrarily to the TS which dives to a maximum of 16 m. Diving involves greater energy expense than surface seizing but it is easier for species with low body/wing ratio (Spear & Ainley, 1998). Therefore, in a perspective of spatial niche partitioning, it is possible that the two species do not segregate with regards to prey items, but spatially in the water column when they forage in the same areas. The WTS is mainly known as a surface feeder (Safford and Hawkins, 2013), though it does show capacity for diving (Burger 2001). The TS sibling species in the Caribbean (*P. lherminieri*) also shows a strong diving activity (Precheur et al in prep). Our results could hypothesize that in a competition situation, WTS and TS differ in diving capacities.

In conclusion, our study highlights marine areas potentially favourable for these two sympatric species, and their differences in terms of foraging distribution. The TS is more confined around the Seychelles and Comoros archipelagos and North of Mozambique Channel, whereas the WTS is more pelagic and spreads throughout the tropical Indian Ocean basin. The habitat suitability maps also underline how suitable areas can vary within seasons and breeding periods, which can be an important factor to account for in the identification of Important Bird Areas at sea (Amorim et al. 2009). Our

results highlight the importance of the Sri Lanka region for the WTS and the Comoros archipelago for the TS during the non-breeding period. The relationship with sub-surface predators has proved to be important for both species; therefore an informed and cautious management of tuna and billfish stock in the Seychelles and Comoros EEZs is particularly recommended in order to maintain a viable population of shearwaters in the region. The spatial segregation between the two species also adds a piece to the puzzle of species interactions, an important information that can be used to inform conservation management actions. In addition, the inter-breeding distribution of the TS overlaps with the breeding range of two other *P. bailloni* subspecies (*P. b. persicus* and *P. b. temptator*); this raises interesting questions in terms of biogeography and competition among subspecies.

Tables

Table 4.1. Details of the tropical (T) and wedge-tailed (W) trips used for the analysis. C = the whole trip was recorded by the geolocator, I = the geolocator stopped before retirement, CR = chick rearing duration, IB = inter-breeding duration, PB = pre-breeding duration.

Sp.	bird id	sex	start track dd/mm/yy	stop track dd/mm/yy	max distance from the colony chick rearing (km)	max distance from the colony inter- breeding (km)	max distance from the colony pre- breeding (km)	trip	year	CR (d)	IB (d)	PB (d)	total (d)
T	GE50797		01/08/12	11/06/13	516	1431	1473	C	2012/13	30	187	95	314
T	GE50761	F	22/08/12	02/01/13		3137		I	2012/13	0	133	0	133
T	GE50745	F	27/08/12	07/03/13		1131		C	2012/13	0	192	0	192
T	GE50760	M	21/08/12	07/03/13		2022		C	2012/13	0	198	0	198
T	GE50747	F	22/08/12	20/03/13		2329		C	2012/13	0	210	0	210
T	GE50746	M	21/08/12	07/03/13		2773		C	2012/13	0	198	0	198
T	GE50758	M	21/08/12	20/03/13		1789		C	2012/13	0	211	0	211
T	GE50776	M	28/05/13	23/08/13		1015		C	2013	0	87	0	87
T	GE50778	F	29/05/13	27/01/14	379	1055		I	2013/14	46	196	0	243
T	GE50779	M	29/05/13	21/07/14	561	2031	534	C	2013/14	63	287	66	418
T	GE50905	M	01/04/14	29/04/14	529			I	2014	28	0	0	28
T	GE50907	F	27/03/14	11/05/14		668		I	2014	0	45	0	45
T	GE50906	F	27/03/14	21/04/14		992		I	2014	0	25	0	25
T	GE50916	F	03/04/14	25/04/14		714		I	2014	0	22	0	22
T	GE50912	F	01/04/14	29/04/14		1668		I	2014	0	28	0	28
T	GE50908	M	27/03/14	27/04/14		1063		I	2014	0	31	0	31
T	GE50915	F	03/04/14	21/05/14		978		I	2014	0	48	0	48
T	GE50929		27/06/14	06/12/14	784	1790		I	2014	31	130	0	162
T	GE34049		27/06/14	13/01/15	846	2160	1093	C	2014	19	135	44	200
T	GE50923	F	10/04/14	21/10/14	1190	1883	1183	C	2014	61	107	24	194
T	GE50926		27/06/14	12/11/14	1025	3592		C	2014	12	125	0	138
T	GE50927		27/06/14	06/01/15		2161	707	C	2014	0	154	37	193
T	GE50928		27/06/14	13/01/15	916	1850	1365	C	2014	59	95	44	200
T	GE50917		07/04/14	24/09/14		1756		C	2014	0	170	0	170
T	GE50918	F	07/04/14	29/09/14		2545		C	2014	0	175	0	175
T	GE50924	M	09/04/14	11/09/14		1368		C	2014	0	155	0	155
W	FS34574		11/03/13	30/06/13	604	3816		I	2013	20	90	0	111
W	FS34770	M	02/03/13	05/10/13	432	3327	1348	C	2013	13	127	75	217
W	FS34582	M	17/03/13	03/09/13		3497	1007	C	2013	0	135	34	170
W	FS34418	M	14/02/13	03/09/13	305	4140	1089	C	2013	9	124	66	201
W	FS34565	M	08/03/13	03/09/13	933	3557	889	C	2013	9	112	56	179
W	FS34427	M	14/02/13	02/10/13		3916	997	C	2013	0	132	97	230
W	FS34791	M	14/02/13	18/09/13		1904	1200	C	2013	0	122	93	216
W	FS34428	M	14/02/13	08/10/13		3460	1053	C	2013	0	136	99	236
W	FS34572	M	09/03/13	09/10/13		3606	909	C	2013	6	107	99	214
W	FS34615	F	10/03/14	04/08/14		4663	880	C	2014	0	134	12	147
W	FS34564	M	04/03/14	29/09/14	727	4576	1391	C	2014	11	103	93	209
W	FS34613	F	10/03/14	09/09/14	318	3170	1127	C	2014	5	112	63	183
W	FS34604	F	06/03/14	15/08/14	489	4260	929	C	2014	5	138	17	162
W	FS34607	F	06/03/14	13/10/14		3003	1138	C	2014	0	112	108	221
W	FS34611		10/03/14	19/08/14		3663	523	C	2014	0	117	44	162
W	FS34620	M	09/04/14	07/10/14	593	3149	1005	C	2014	7	59	113	181

Table 4.2. Average (\pm SD) values of environmental variables used for the habitat selection analysis per each period and each kernel 95% and 50%. TS = tropical shearwater, WTS = wedge-tailed shearwater, SE = south-east monsoon season, NW = north-west monsoon season.

species (season)	period (kernel)	chlrophyll (mg/m ³)	bathymetry (m)	SST (°)	slope (°)	wind (m/sec)	Tuna catch (MT)
WTS	non-breeding (50)	0.104 (\pm 0.031)	3980 (\pm 1105)	29.1 (\pm 0.57)	0.23 (\pm 0.23)	83 (\pm 11)	2043 (\pm 4066)
	non-breeding (95)	0.1 (\pm 0.131)	3917 (\pm 1039)	28.63 (\pm 1.19)	0.21 (\pm 0.19)	92 (\pm 24)	2400 (\pm 10079)
	chick-rearing (50)	0.107 (\pm 0.023)	2897 (\pm 1282)	28.95 (\pm 0.17)	0.5 (\pm 0.24)	54 (\pm 4)	9460 (\pm 5220)
	chick-rearing (95)	0.111 (\pm 0.037)	3664 (\pm 1131)	28.9 (\pm 0.28)	0.32 (\pm 0.24)	52 (\pm 4)	11019 (\pm 6306)
	pre-breeding (50)	0.246 (\pm 0.085)	3023 (\pm 1039)	26.09 (\pm 0.31)	0.35 (\pm 0.21)	108 (\pm 13)	8265 (\pm 6080)
	pre-breeding (95)	0.207 (\pm 0.17)	3545 (\pm 1085)	26.22 (\pm 0.83)	0.33 (\pm 0.22)	112 (\pm 19)	7316 (\pm 8482)
TS (NW)	non-breeding (50)	0.127 (\pm 0.03)	4070 (\pm 1135)	28.56 (\pm 0.2)	0.30 (\pm 0.25)	48 (\pm 5)	15599 (\pm 10707)
	non-breeding (95)	0.161 (\pm 0.189)	3655 (\pm 1150)	28.38 (\pm 0.5)	0.26 (\pm 0.21)	59 (\pm 10)	9432 (\pm 9386)
	pre-breeding (50)	0.125 (\pm 0.03)	2251 (\pm 1246)	28.67 (\pm 0.09)	0.66 (\pm 0.14)	52 (\pm 3)	8481 (\pm 7283)
	pre-breeding (95)	0.128 (\pm 0.025)	3761 (\pm 1037)	28.54 (\pm 0.19)	0.29 (\pm 0.23)	52 (\pm 7)	13446 (\pm 9460)
TS (SE)	non-breeding (50)	0.2 (\pm 0.049)	3311 (\pm 1097)	27.23 (\pm 0.47)	0.40 (\pm 0.22)	102 (\pm 14)	9661 (\pm 6417)
	non-breeding (95)	0.172 (\pm 0.101)	3914 (\pm 1067)	26.82 (\pm 1.18)	0.33 (\pm 0.30)	104 (\pm 20)	9033 (\pm 10637)
	chick-rearing (50)	0.24 (\pm 0.075)	2225 (\pm 974)	27.56 (\pm 0.27)	0.62 (\pm 0.14)	91 (\pm 5)	9158 (\pm 8168)
	chick-rearing (95)	0.19 (\pm 0.046)	3569 (\pm 1057)	27.57 (\pm 0.64)	0.35 (\pm 0.22)	95 (\pm 15)	12232 (\pm 9709)
	pre-breeding (50)	0.21 (\pm 0.052)	2845 (\pm 1057)	27.58 (\pm 0.38)	0.53 (\pm 0.18)	92 (\pm 9)	11281 (\pm 6180)
	pre-breeding (95)	0.159 (\pm 0.091)	3911 (\pm 855)	27.97 (\pm 1.08)	0.24 (\pm 0.19)	90 (\pm 23)	9828 (\pm 8543)

Table 4.3. ENFA analysis. Marginality and specialization values per each species, period and season. NW = north-west monsoon season, SE = south-east monsoon season.

period	Axes	chl	bathy	SST	slope	wind	tuna
WTS							
chick-rearing	Marginality	-0.009	0.163	0.263	0.368	-0.671	0.565
	Specialization	-0.352	-0.093	-0.576	0.212	-0.522	-0.467
non-breeding	Marginality	-0.251	-0.297	0.642	-0.252	-0.416	0.445
	Specialization	0.787	0.153	0.506	-0.148	0.278	-0.006
pre-breeding	Marginality	0.161	0.126	0.178	0.298	0.167	0.899
	Specialization	-0.813	0.285	-0.398	-0.032	-0.203	0.233
TS (NW)							
non-breeding	Marginality	0.067	-0.09	0.299	0.052	-0.53	0.782
	Specialization	-0.142	0.121	-0.922	-0.002	-0.279	0.189
pre-breeding	Marginality	0.071	0.216	0.302	0.344	-0.511	0.69
	Specialization	-0.045	0.125	-0.93	-0.01	-0.3	0.159
TS (SE)							
chick-rearing	Marginality	0.413	0.39	0.139	0.592	-0.148	0.532
	Specialization	0.025	0.021	-0.792	-0.072	-0.598	0.087
non-breeding	Marginality	0.201	0.007	0.215	0.239	0.02	0.924
	Specialization	0.009	-0.058	0.967	0.011	0.079	-0.232
pre-breeding	Marginality	0.192	0.183	0.251	0.338	-0.224	0.838
	Specialization	-0.139	0.166	-0.919	-0.064	-0.214	0.24

Figures

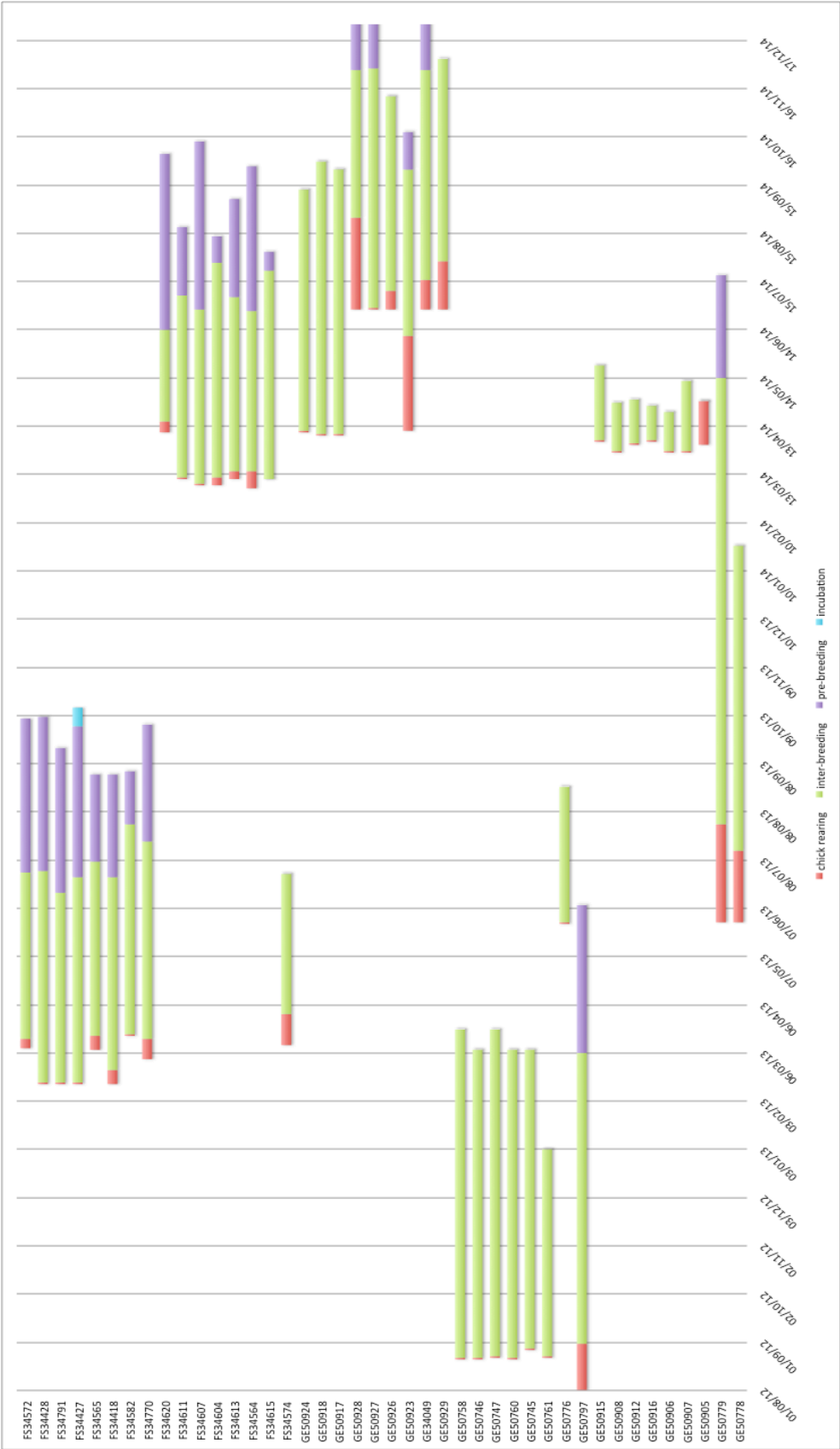


Figure 4.1. Periods and duration of the trips selected for the data analysis. The id of the birds starting with FS and GE refers to the wedge-tailed and to the tropical shearwater respectively.

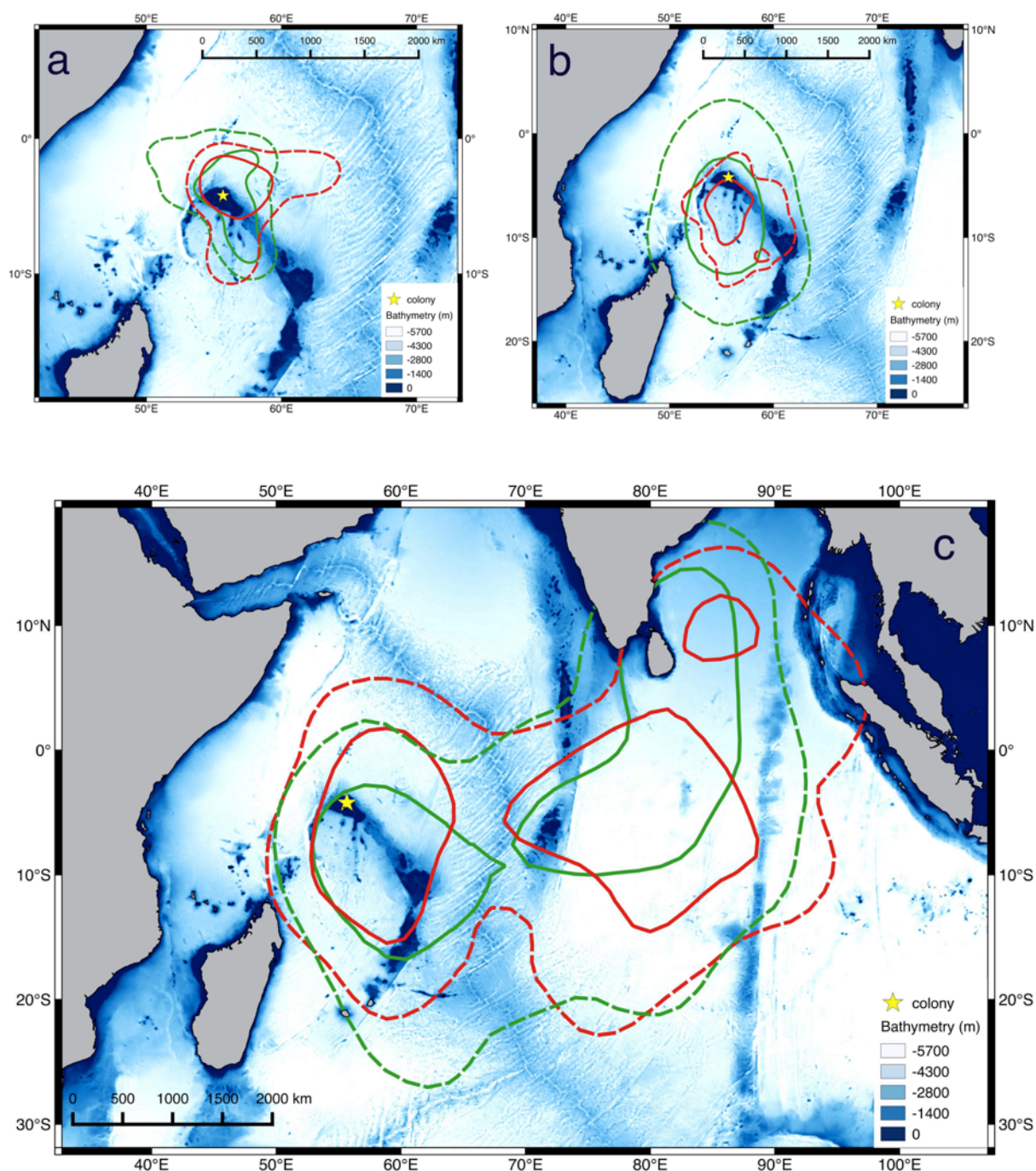


Figure 4.2. Wedge-tailed shearwater kernels during chick rearing (a), pre-breeding (b) and non-breeding period (c). The dashed line represent the 95% and the continuous line the 50% density kernel. In red and green are indicated 2013 and 2014 respectively.

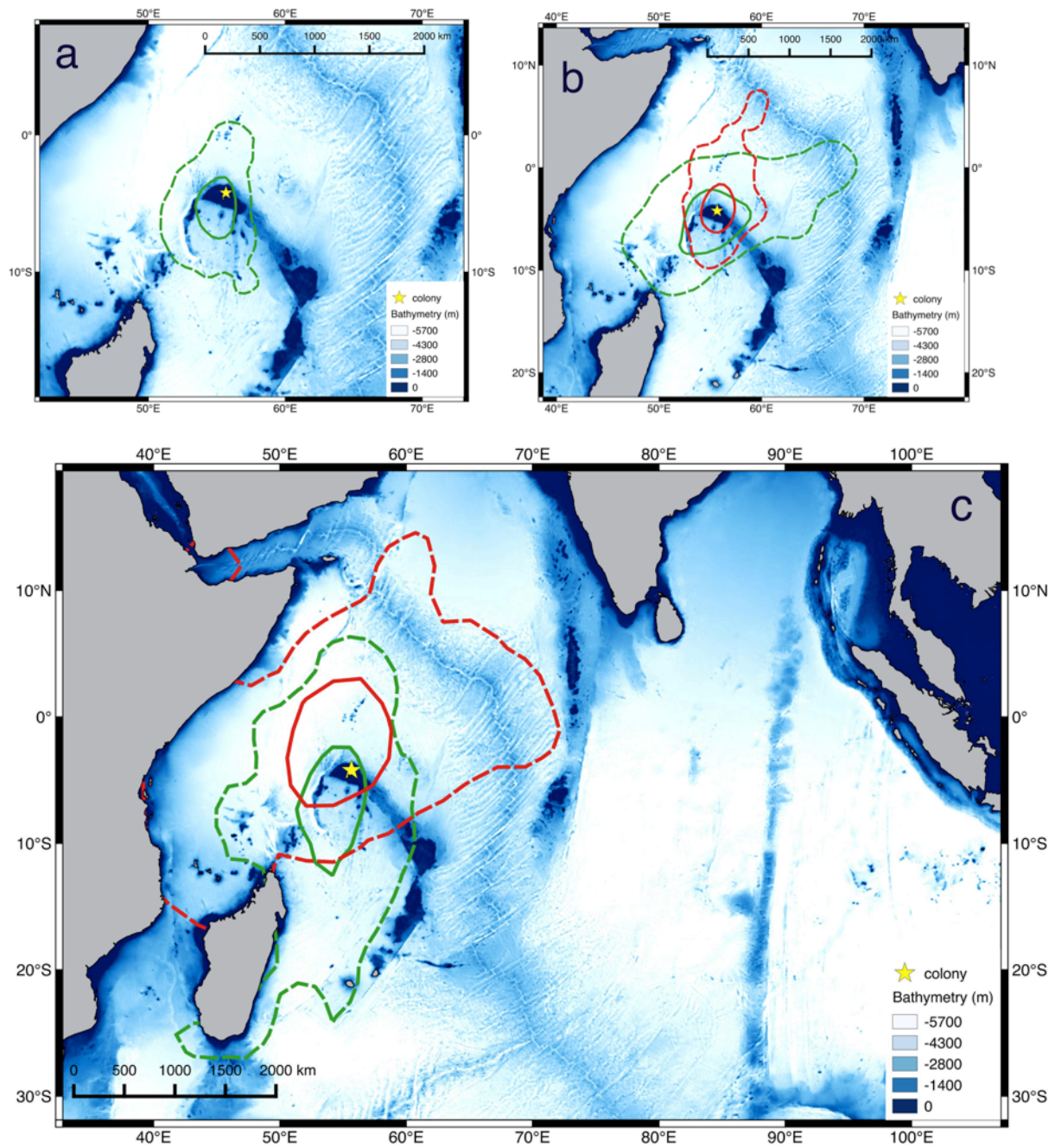


Figure 4.3. Tropical shearwater kernels during chick rearing (a), pre-breeding (b) and non-breeding period (c). The dashed line represent the 95% and the continuous line the 50% density kernel. In red and green are indicated the NW and SE monsoon seasons respectively.

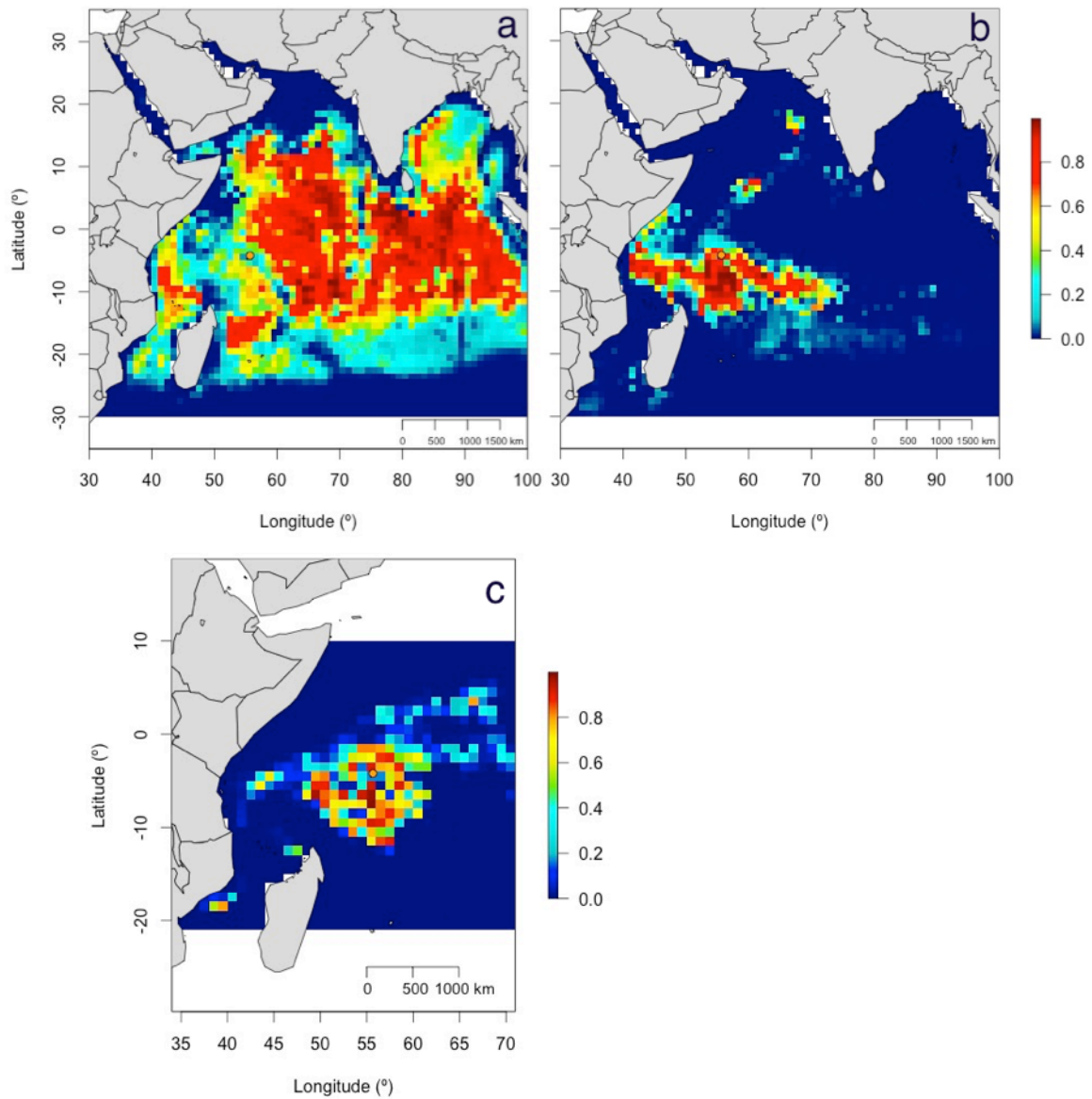


Figure 4.4. Wedge-tailed shearwater. Habitat suitability maps during the non-breeding (a), pre-breeding, (b) and chick rearing periods (c). The unit measure is the probability (from 0 to 1) to find the species in a given area.

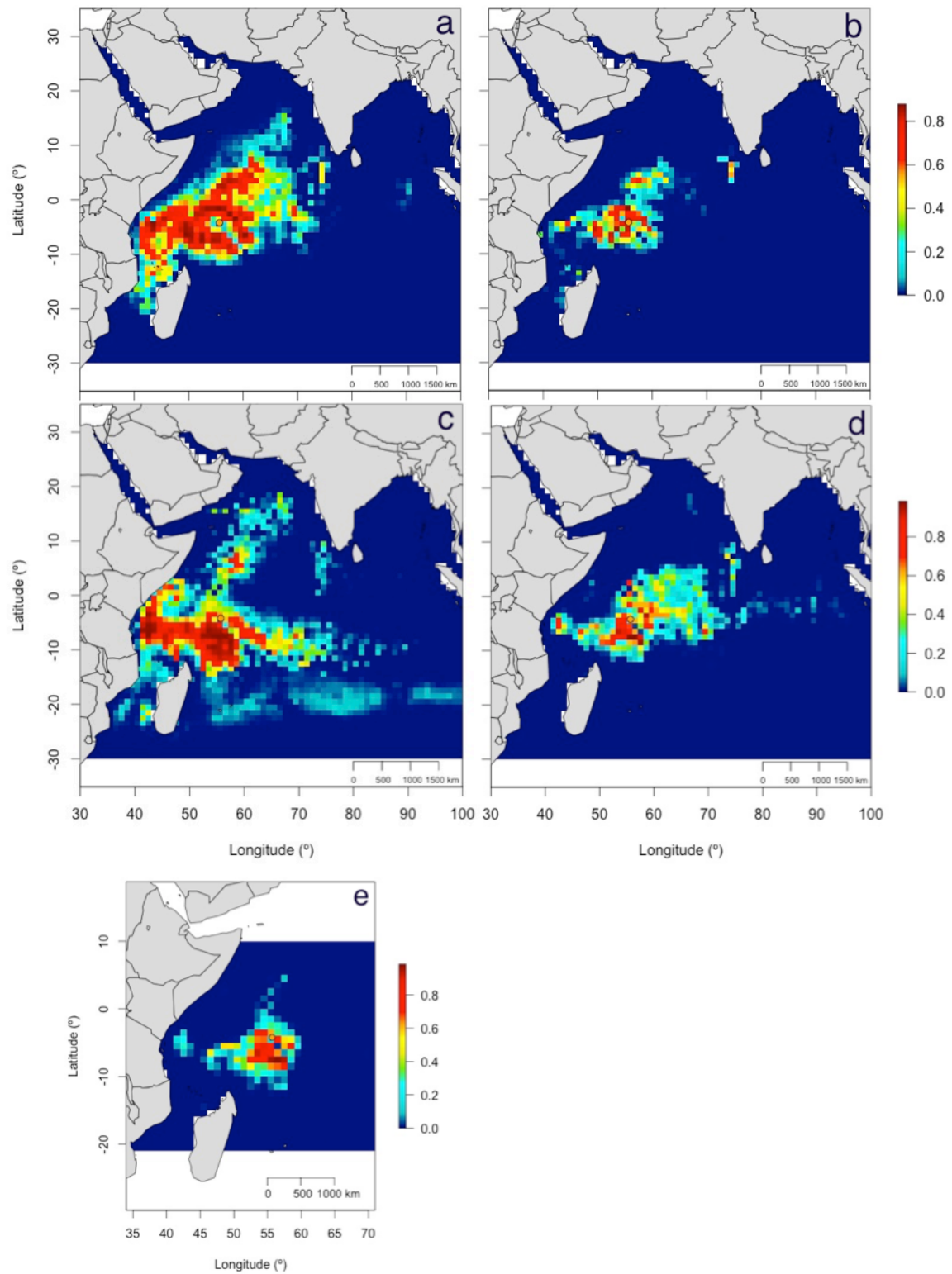


Figure 4.5. Tropical shearwater. Habitat suitability maps during the NW monsoon in non-breeding (a) and pre-breeding (b) periods; and during the SE monsoon in non-breeding (c), pre-breeding (d) and chick-rearing (e) periods. The unit measure is the probability (from 0 to 1) to find the species in a given area.

External Supplementary Materials (ESMs)

ESM 4.1. Wedge-tailed and tropical shearwater habitat preferences

The following figures show the outcome of the ENFA analysis for wedge-tailed (Figure ESM 4.1A) and tropical (Figure ESM 4.1B and C) shearwaters respectively. On the left side, the white histograms show the distribution of available resource per each environmental variable whereas the grey histograms show the distribution of resource units used by the individuals. On the right side, the results of the ENFA are represented with the main biplot panels. The dark grey polygon shows the distribution of the resource units used by the species and the light grey polygon represent the position of the available resource units. The abscissa is the marginality and it indicates the direction where the centroid of the distribution of utilization weights (white dot) is the furthest from the centroid of the distribution of available weights (origin of the axes). The ordinate is the first specialization axis, the direction where the variance of the utilization distribution is the smallest relative to the variance of the availability distribution. The arrows are the projections of the environmental variables. The ENFA biplot contains two inserts: the values of marginality and specialization per each variable and the histogram with the eigenvalues of specialization. In our cases one axis of specialization explains most of the specialization and is kept for the analysis.

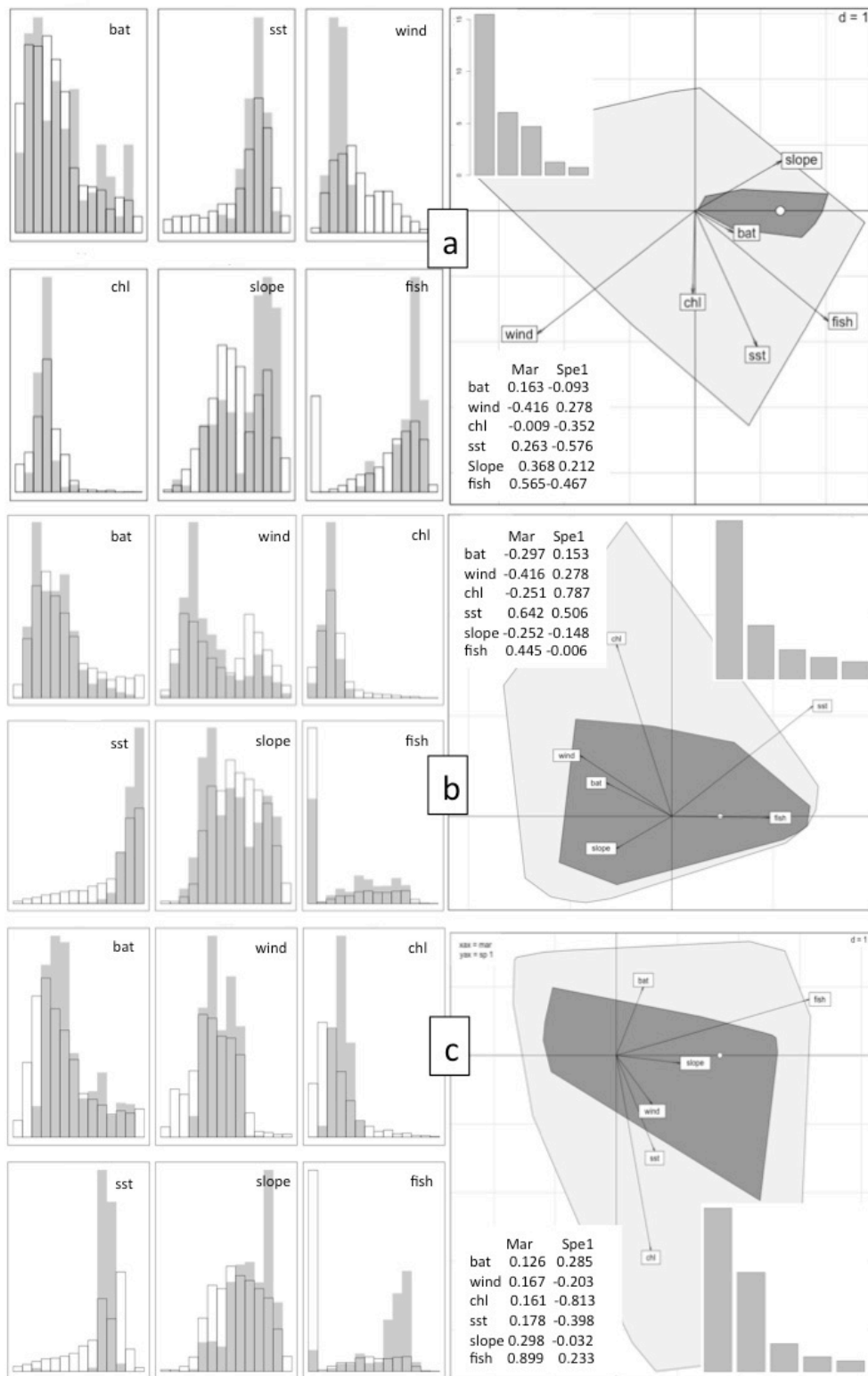


Figure ESM 4.1A. Wedge-tailed shearwater. Habitat preferences during chick-rearing (a), non-breeding (b) and pre-breeding (c) periods. Fish = MT of tuna and billfish caught.

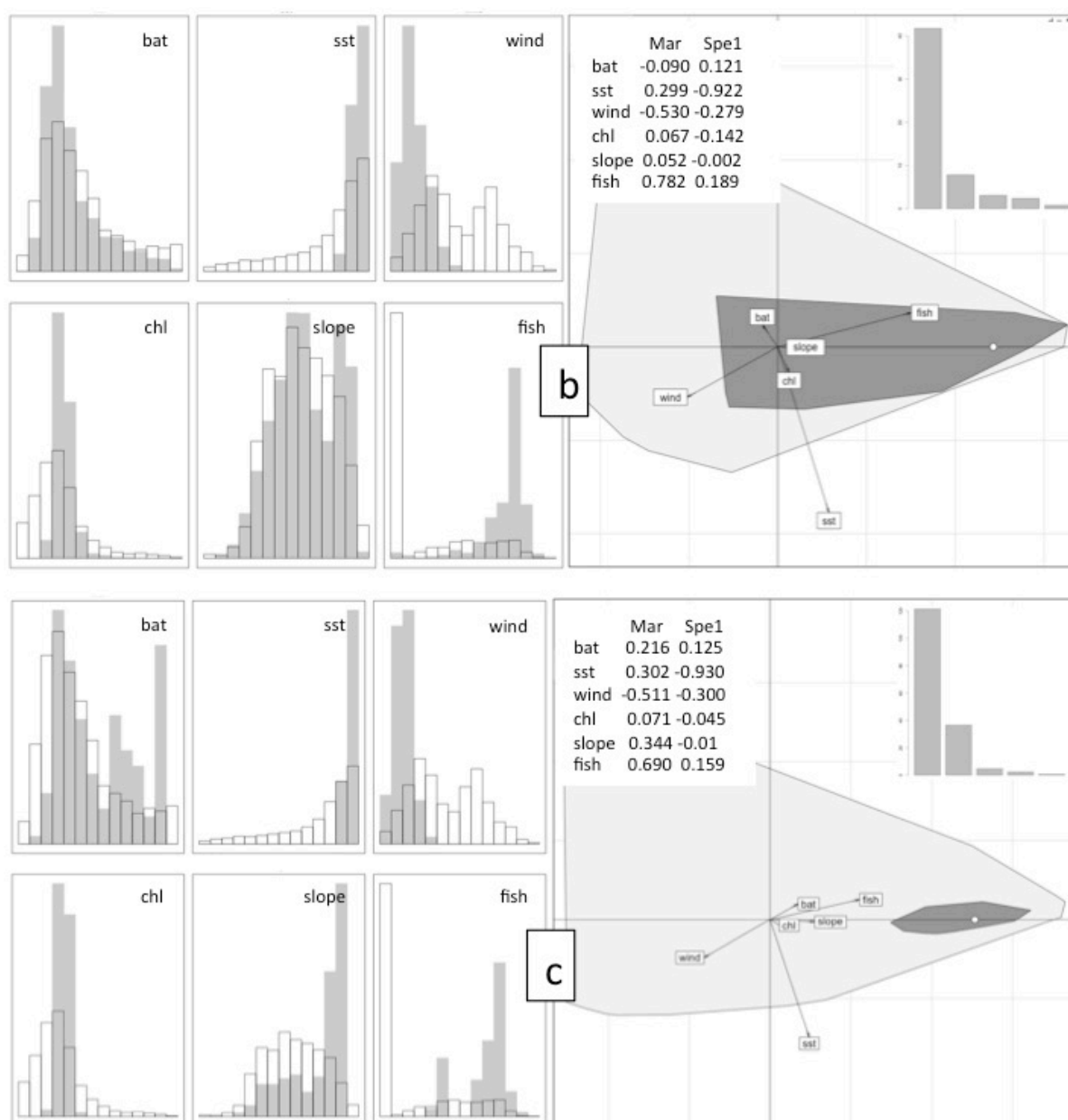


Figure ESM 4.1B. Tropical shearwater. Habitat preferences during non-breeding (b) and pre-breeding periods in the NW monsoon season. Fish = MT of tuna and billfish caught.

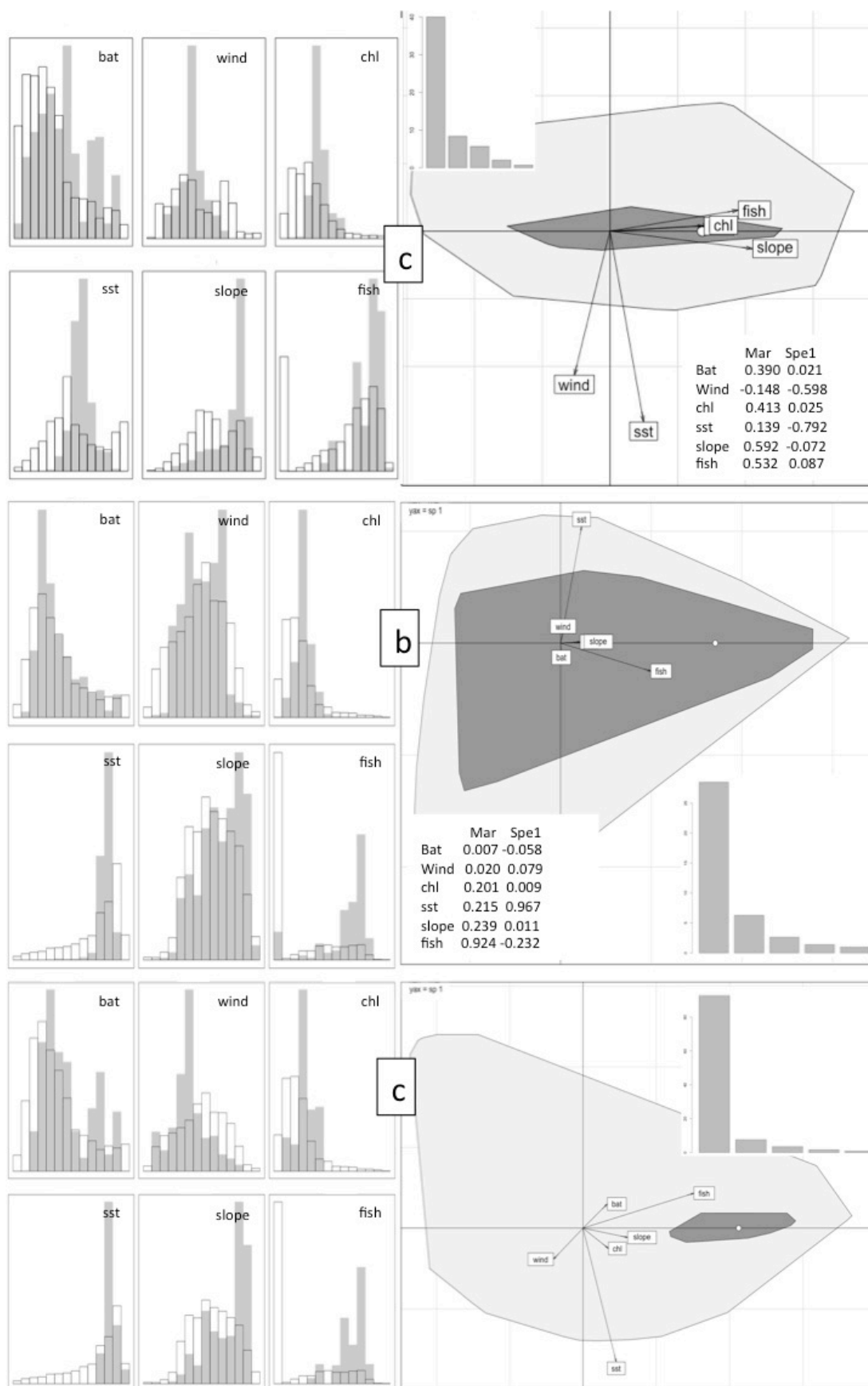


Figure ESM 4.1C. Tropical shearwater. Habitat preferences during chick-rearing (a), non-breeding (b) and pre-breeding periods in the SE monsoon season. Fish = MT of tuna and billfish caught.

CHAPTER 5

Movement Patterns and Habitat Selection of Wedge-Tailed Shearwaters (*Puffinus pacificus*) Breeding at Aride Island, Seychelles

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Manuscript published: Cecere, J. G., Calabrese L., Rocamora G., Catoni C. 2013. Movement patterns and habitat selection of Wedge-tailed Shearwaters (*Puffinus pacificus*) breeding at Aride Island, Seychelles. Waterbirds 36.4: 432-437.

Abstract

Seabird movements during foraging trips and their preference for particular areas have recently been the focus of many studies aimed at gaining a better understanding of the ecological requirements of several species. During the last decade, the use of new devices, such as Global Positioning System (GPS) devices and geo-locator loggers, has allowed researchers to perform more investigations of this type. GPS devices were used on Wedge-tailed Shearwaters (*Puffinus pacificus*) breeding on Aride Island, Seychelles, to identify the main foraging areas used during early chick-rearing and to assess at-sea foraging habitat selection. Thirteen foraging trips were recorded, 61.5% of which lasted one day. One main foraging area, located approximately 100 km east of the colony just outside a granitic bank characterized by upwelling and higher values of primary production compared to surrounding areas, was identified. The foraging area size (3,313 km²) was much smaller than that identified during late chick-rearing (160,000 km²) in a previous study. This is probably due to the exigency to feed chicks more regularly and hence to find foraging areas closer to the colony during the early chick-rearing. The identification of key marine conservation areas, like those identified in this study, is a priority for designating marine Important Bird Areas and identifying habitat management measures. The results of this study should be relevant for the development of conservation plans for Wedge-tailed Shearwaters and for other seabirds in the area.

5.1 Introduction

During the last decade, the use of Global Positioning System (GPS) devices and remote sensing technology has provided scientists with a large amount of information about bird movements, even over the open sea (Wakefield *et al.* 2009). Furthermore, the ability to link accurate bird positions to remote sensing data has facilitated the analysis of habitat selection and use by pelagic bird species (Wakefield *et al.* 2009). This kind of information is particularly relevant for conservation purposes, and GPS telemetry has been included in the standard methodology adopted to identify marine Important Bird Areas around the globe (BirdLife International 2010).

While several studies have been published about the habitat use of different seabird species (Wakefield *et al.* 2009), to our knowledge, nobody has yet deployed this technology to both analyze movement patterns and determine habitat selection of Wedge-tailed Shearwaters (*Puffinus pacificus*). Wedge-tailed Shearwaters are a medium-sized tubenose species that ranges across the tropical Pacific and Indian Oceans where threats to the populations include unsustainable levels of fish exploitation, persecution, predation by invasive species and the over-exploitation of tuna fisheries (Brooke 2004). Catry *et al.* (2009) were the first to document the movements of Wedge-tailed Shearwaters using geo-locator loggers (GLS) during late chick-rearing, non-breeding and pre-breeding periods. This study focuses on the same population, breeding at Aride Island Nature Reserve, Seychelles, but during early chick-rearing, a critical period during which the chicks of shearwater species generally need to be fed often (Klomp and Furness 1992), thus forcing adults to find prey near the colony (Cecere *et al.* 2013). In addition, instead of GLS, we used GPS technology that allowed us to determine bird position with a much greater accuracy and resolution.

The objectives of this study are to: 1) identify the main foraging areas exploited by Wedge-tailed Shearwaters breeding at Aride Island during the early chick rearing period and compare these areas with those used during the late chick-rearing period as assessed by Catry *et al.* (2009); and 2) investigate whether birds from Aride Island select upwelling areas characterized by high values of primary production. Such environmental features are normally associated with the presence of large fish schools (Blanchette *et al.* 2009).

5.2 Materials and Methods

Study Area

The study was carried out on Aride Island (4° 12' 46" S, 55° 39' 53" E), the northernmost granitic island in the Seychelles. Aride Island occurs within the Seychelles bank, which forms the northern part of the Mascarene plateau, an arc aseismic ridge extending south 2,000 km from the Seychelles to La Réunion and west through the Amirantes between the Somali and Mascarene Basins. The Seychelles bank is mostly shallower than 125 m and is characterized by an enhanced oceanic productivity caused by interaction of the banks with the South and North Equatorial Currents (Tomczak and Godfrey 2003). This interaction is

likely important for ocean food webs as indicated by seabirds and whales using the Seychelles Basin (Obura et al. 2012).

The island is a nature reserve of approximately 73 ha, where the only human inhabitants are the reserve's staff and volunteers. The island hosts over one million seabirds belonging to 10 species (Skerrett and Disley 2011). The colony of Wedge-tailed Shearwaters consists of an estimated 18,500 pairs (Rocamora and Skerrett 2001). The Wedge-tailed Shearwaters of the Aride Island colony bred rather asynchronously with both eggs and 1-15 day-old chicks in the nests during mid-October and early November 2012 when the study was carried out (J. G. Cecere, pers. obs.). The colony is mainly located along the southern part of the island. Sampled nests were located throughout the colony (Range = 2-553 m distance between sampled nests). Only nests with young chicks with down and no growing feathers on the tail and wings were used for the study.

GPS Logger Deployment

Wedge-tailed Shearwaters breed in burrows, making it very easy to catch the adults by hand during the night just after they have fed their chicks. Wedge-tailed Shearwaters were banded and weighed and a mini-GPS logger (see below) was attached to the back feathers using 3-4 strips of Tesa marine cloth tape (Wilson et al. 1997). Total handling time was kept below 10 min, and individuals were returned to their nests immediately afterward. Nesting burrows are usually not deep, allowing researchers to see, keep and weigh the chick while an adult was tagged.

Nests were monitored every night from dusk to dawn, checking each target nest four or five times per night. Once a bird with a GPS device returned to the nest, it was recaptured and the GPS logger removed by peeling away the tape from the feathers. Mini-GPS loggers with strip antennas (Technosmart Europe) were used. The GPS loggers carried two different batteries, one 160 mA and one 250 mA, so the final weight of the devices (waterproof covering and Tesa tape included) was 11 and 12.6g, respectively. The deployment of the lighter GPS loggers allowed for tracking of lighter birds, despite the shorter life-span of these devices. Device weight (band excluded) averaged 3.45% of the bird's weight (Range = 3.1-3.7%), so that Wedge-tailed Shearwaters should not have been influenced by the extra-mass (Passos et al. 2010). All GPS loggers were configured to record at the same time both the position and the instantaneous speed of the marked individual every 10 min. A foraging trip began with a departure from the nest and ended at the first return to the nest.

Data Analyses

The main areas used by tracked birds were identified by means of kernel analyses using only GPS positions with an instantaneous speed of less than 9 kph. This threshold has been used to identify positions where Manx (*P. puffinus*) and Scopoli's (*Calonectris diomedea*) shearwaters (Guilford et al. 2008; Cecere et al. 2012) were using the environment for either resting, searching for food, or diving, thus excluding positions where the birds were travelling. Fixed kernels were computed at the probability level of 50%, identifying the core areas used by breeders during foraging trips.

One hundred random points were generated within identified core foraging areas that were considered representative of the habitat used. These 100 random points were compared to 500 random points considered representative of available sea habitat to investigate whether breeding Wedge-tailed Shearwaters selected particular environmental characteristics during foraging trips. These 500 random locations were generated within a buffer zone created around the colony of Aride Island with a radius of 206 km. This radius was determined using the farthest recorded position of tracked birds from the breeding colony (186 km), enlarged with a 20-km buffer (the likely olfactory detection distance for pelagic birds; Nevitt 2008). Random points for both used and available areas were randomly generated using ArcGIS (Environmental Systems Research Institute 2008).

Three variables were selected to characterize both used and available random point locations: 1) sea depth, obtained from the General Bathymetric Chart of the Oceans (GEBCO 08) of the British Oceanographic Data Centre as a 30 arc-second grid (approximately 1 km); 2) minimum distance to the edge of granitic bank; and 3) net primary production data (standard Vertically Generalized Production Model (VGPM)), from the Ocean Productivity website. This data have a spatial resolution of 10 arc-min (approximately 18 km) and include sea surface temperature, chlorophyll and photosynthetically active radiation values (Behrenfeld and Falkowski 1997). For each location, we extracted the primary production value of the month in which tracking was performed.

All spatial analyses were performed using ArcGIS (Environmental Systems Research Institute 2008) with the help of different tools: the kernel analysis was performed with the Home Range Tool (Rodgers et al. 2007); net primary production raster was converted using Marine Geospatial Ecology Tools (Roberts et al. 2010); the extraction of raster values for each point was obtained using the Spatial Analyst Tools package; while all distances were calculated using the ET Geo Wizards package (Tchoukanski 2012). Since all environmental variables were strongly correlated, we chose to use only one of them in the following analysis to avoid problems in parameter estimation (Zuur et al. 2007). Hence, habitat selection was assessed using logistic regression with the use/availability of each location being treated as the dependent variable and net primary production being treated as the independent variable (R Development Core Team 2012). The relationship between the maximum distance covered by breeders during their foraging excursion and the weight of the chick at the moment of adult departure was analyzed by linear regression (R Development Core Team 2012).

5.3 Results

A total of 14 Wedge-tailed Shearwaters were tagged, but unfortunately four individuals lost their GPS logger. Two consecutive trips were recorded for one bird and three consecutive trips for a second bird. The remaining eight individuals were recorded during only one foraging trip (Table 5.1). Eleven foraging trips out of 13 were complete, with recorded positions from the beginning to the end. The remaining two trips were incomplete since the device switched off before the first return (after 3 and 4 days), and the birds were re-caught after 8 and 9 days respectively from GPS deployment. In these two cases, we could not determine the temporal length of the trip since we could not conclusively determine if the bird came back to the colony before it was re-caught. Most (61.5%) of the trips lasted 1 day,

15.4% lasted 2 days and the remaining 23.1% lasted > 3 days (Table 5.1). All birds took the same main direction from the colony, heading east (Figure 5.1). Kernel utilization distribution at 50% identified one core area of 3,313 km², the centroid of which was located about 117 km east of the breeding colony. The exploited area was located just outside the granitic bank, close to its boundaries (Fig. 5.1). Compared to marine habitat available, breeding Wedge-tailed Shearwaters selected a foraging area characterized by higher values of primary production ($z = 6.203$, $P < 0.001$). The use range was 323.5-505.2 mg C m⁻² day⁻¹ (average = 404.43 ± 53.5 mg C m⁻² day⁻¹) while the available range was 267.1-538.7 mg C m⁻² day⁻¹ (average = 356.5 ± 67.1 mg C m⁻² day⁻¹).

Chick weight averaged 198.2 g (Range = 34.4-445.2, $n = 9$). Using a log fit, the maximum distance covered by breeders during foraging trips was positively related the chick weight (linear regression: $t = 3.35$, $R^2 = 0.616$, $P = 0.012$). The variance accounted for chick weight was 61.6%.

5.4 Discussion

During the chick-rearing phase, several pelagic bird species perform a dual foraging strategy, alternating short trips used for chick provisioning and longer trips mainly used for self-provisioning (Weimerskirch et al. 1994). This behavior allows birds to balance the need of regularly visiting the colony on the one hand, with accessing better foraging areas farther from the colony on the other hand. Normally, during the early chick-rearing period, chicks need to be fed often and regularly, forcing breeders to make short trips and, in some cases, to exploit less profitable areas than those exploited with longer trips (see Cecere et al. 2013). Congdon et al. (2005) have described a dual foraging strategy for Wedge-tailed Shearwaters breeding on Heron Island, Australia, with foraging adults performing short-trip cycles of multiple 1- to 4-day trips followed by a single long trip of approximately 8 days. In the current study, only one trip out of 13 (7.7%) lasted more than 4 days (a second one may have lasted more than 4 days, but the GPS ran out of battery power before individual returned). The infrequent occurrence of long lasting foraging trips (> 4 days), normally used by most shearwater species for self-provisioning (Weimerskirch et al. 1994), could be due to the opportunity for self-provisioning during shorter trips (≤ 4 days). A specific study analyzing the length of foraging trips carried out throughout the whole chick-rearing period will be required to test this hypothesis. It is possible that long lasting trips may occur more frequently during the late chick-rearing period. This hypothesis is supported by the positive relationship between chick weight and maximum distance covered by adults during their foraging excursions.

Despite the limited sample size, it is clear that birds always flew to the east, presumably to forage. The ability of long-lived seabirds to head from the breeding colony toward favoured and profitable foraging areas is well known (Weimerskirch 2007). In this study, all tagged birds exploited the same area located just beyond the granitic bank in an upwelling area characterized by higher values of primary production compared to the surrounding marine habitat.

The exploited area size was much smaller than that identified during late chick-rearing for Wedge-tailed Shearwaters breeding on Aride Island (3,313 vs. 160,000 km²; Catry et al. 2009). Considering the similar sample size of the two studies (10 and 9 birds

respectively), the difference might be due to the higher accuracy of GPS technology, compared to that of GLS technology used by Catry et al. (2009). However, since we cannot exclude the dual foraging strategy in the Aride Island population, the difference in size could also be due to the different period investigated. Late chick-rearing could indeed be characterized by longer trips, which could allow birds to explore larger areas, although longer trips do not necessarily imply the exploitation of a larger area since birds could simply travel to a more distant, concentrated region to feed.

Overall, GPS technology proved to be a good tool to study this relatively small shearwater species. Nevertheless, we have to note that a good number of individuals managed to peel off the device (29%), which was lost despite the experience of the authors with GPS deployment. Most of the re-trapped tagged Wedge-tailed Shearwaters, indeed, had pieces of the Tesa tape removed and in two cases the device was about to fall off during the re-trapping.

Despite the small sample size, all tracked birds went to such a consistent fishing ground that we believe our results could be considered reliable. Despite being rated as a species of Least Concern according to the IUCN red list, there is evidence of population decline among Wedge-tailed Shearwaters (BirdLife International 2010). The identification of key foraging areas, like those used by breeders from Aride Island during early chick-rearing, is a priority for habitat management and conservation action plans for pelagic seabirds.

5.5 Acknowledgments

We are extremely grateful to Aride Island Nature Reserve staff and volunteers, particularly Gwen Maggs, Rebecca Melville, Andrew Murray and Emmanuel Lesperance for their help during fieldwork; Pierre-André Adam, Dixon Bastienne and other ICS Head office staff on Mahé for general support; and Simona Imperio (RicercaFauna) for her useful suggestions. A special thanks to Vincent Bretagnolle for his critical review of the manuscript. This work was carried out in collaboration with ISPRA, was conducted as part of the Shearwater Research Project of the Island Conservation Society, and was conducted in partnership with Centre Nationale Recherche Scientifique-Chizé and Foundation Total. Capture and handling of birds were conducted under the Seychelles Bureau of Standards authorization (Research Permit N°A0157). We wish to thank Seychelles authorities and all the organizations and individuals that helped us obtain the permit.

Tables

Table 5.1. Summary data for 10 tracked Wedge-tailed Shearwaters. Parameters are: Device (%) = proportion of device (including waterproof covering and Tesa tape) to each marked individual's weight; Trip Number = number of recorded consecutive trips; % Tracked Days = proportion of tracked days of the total number of days the marked individual spent with the device; and Max Distance (km) = Euclidean distance from the breeding colony and farthest recorded location.

Band Number	Weight (g)	Device (%)	Trip Number	Trip Duration (Days)	% Tracked Days	Trip Start	Max Distance (km)
FS34545	357.8	3.5	1	1	100	24/10/12	87.89
			1	2	100	25/10/12	157.97
FS34548	360.1	3.5	2	1	100	27/10/12	139.43
			3	1	100	28/10/12	137.24
FS34549	366.8	3.4	1	> 4	44	26/10/12	185.73
FS34552	294	3.7	1	1	100	26/10/12	85.69
FS34554	370.8	3.4	1	1	100	27/10/12	119.99
FS34555	383.7	3.3	1	> 3	38	27/10/12	176.93
FS34558	364.6	3.5	1	1	100	29/10/12	133.25
			1	1	100	28/10/12	101.36
FS34560	342.9	3.7	2	2	100	29/10/12	118.19
			1	1	100	30/10/12	147.01
FS34561	406.8	3.1	1	1	100	30/10/12	147.01
FS34562	368.7	3.4	1	4	100	29/10/12	123.23

Figures

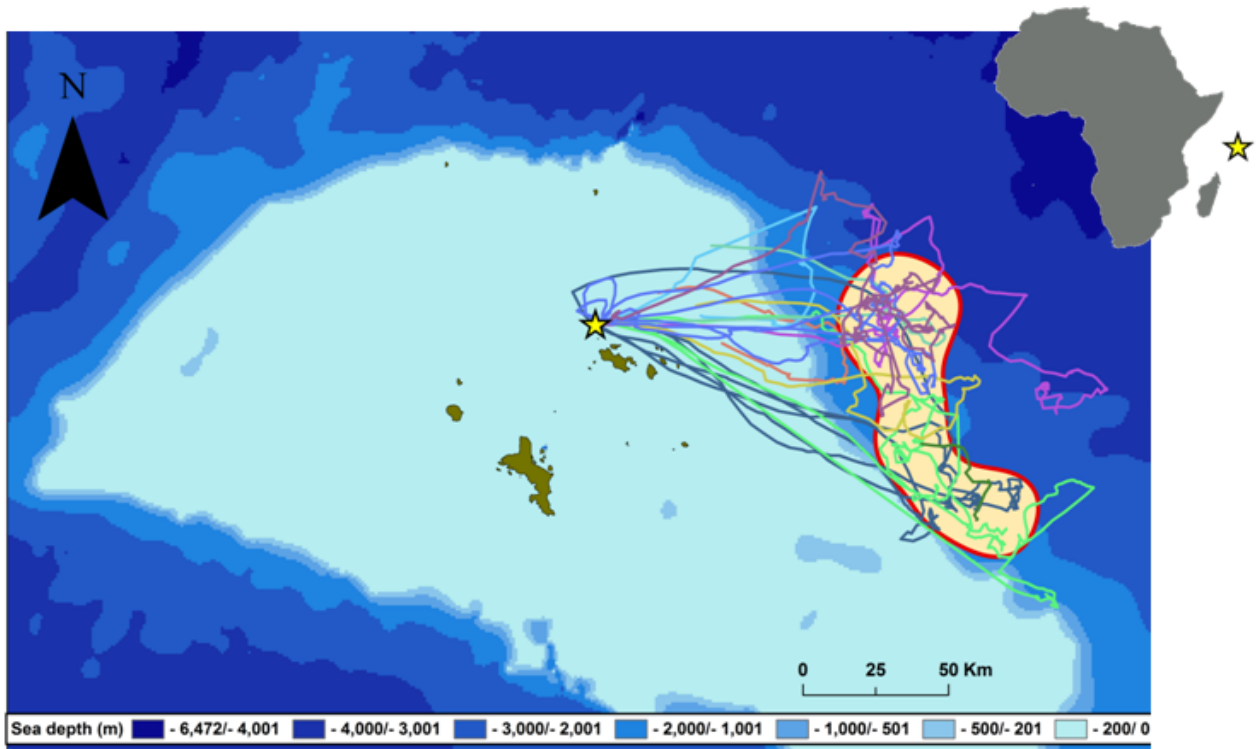


Figure 5.1. Location of Aride Island, Seychelles (star in center) and tracks of foraging excursions of 10 breeding birds recorded during chick-rearing (13 foraging trips). The core area (fixed kernel analysis at 50%), calculated with all the recorded positions with instantaneous speed $< 9\text{km/h}$, is represented in gray; the islands of the granitic archipelago in black; and the boundary of the granitic bank with a broken line. On the top right corner, the position of Aride Island in relation to the Africa continent is shown by a star.

CHAPTER 6

General Discussion

There is little doubt, among seabirds conservationists about the fundamental role played by seabirds and megafauna in general as indicators of the health of prey populations and of the marine ecosystem in general (Furness and Camphuysen, 1997; Frederiksen et al., 2006). Whilst some seabird species are critically endangered with low populations sizes, an increasing proportion of those which are still very abundant appear to be declining (BirdLife International, 2013; Croxall et al. 2012). This identifies many seabirds as conservation priority species according to Caughley's (1994) paradigms. However, because of some of their life history traits, mechanisms taking place within seabirds' populations are difficult to assess and require long-term studies (Bradley et al. 1991).

Assessing population estimates within long-term studies is a very powerful tool in seabirds conservation (Bibby et al. 2012) as changes in numbers and range can be analysed in relation to environmental features, direct threats (e. g. poaching of adults, young and eggs) and success or failure of conservation management policies in protected areas (Bibby et al. 2012; Sutherland et al. 2004). However, the knowledge of seabirds' species trends is difficult information to obtain as long term population monitoring is rare and difficult to set up and maintain (Lindenmayer and Likens 2009; Welsh et al. 2000). Nevertheless, when this information is known, it often associates seabirds with the second Caughley (1994) paradigm of population decline, which gives seabirds an important place within other categories of global conservation concerns (BirdLife International, 2013). As previously mentioned, seabirds are now the most threatened bird group (BirdLife International, 2013; Croxall et al. 2012), in particular the order of the Procellariiformes (Jones and Kress 2012) which comprises 45% of threatened species (Sydeman et al. 2012).

According to present conservation debates, and to the postulates of Soulé (1985, see chapter 1), seabirds should definitely be protected as an important part of the marine ecosystem, given that diversity of life (biodiversity) is always an important value, and also that some seabirds occur at certain sites in concentrations of international importance which are key to identify Important Bird Areas (Fishool & Evans, 2001). However, one may argue that from the new conservation science point of view, seabirds should be less important than species which give direct benefits to humans; in fact in a "triage" process (Sekercioglu 2006; Grémillet and Charmantier 2010; Wenny et al. 2011) they could not be considered among the conservation priorities. At present, studies assessing species and communities ecosystem services are increasing and some of them actually proved that

marine birds can provide as many (ecosystem) services than any other species group (Whelan et al., 2008).

Given the conservation importance of seabirds, knowledge about their status is becoming more and more a priority. Our findings are of particular interest, not only because we focus on species which belong to the most threatened order of birds, for which knowledge is still limited, but also because we use a “full life cycle” approach where almost all life stages are examined and the potential competition among the two species is taken into account. The 2-competing species approach is novel and can be important to highlight trade-offs in conservation decision-making. Moreover, we consider nearly the “full life cycle”, which is not only rare in conservation, but in ecology altogether (Furness and Camphuysen 1997; Heppell et al. 2000). This approach is particularly complicated to perform on species that are difficult to follow throughout their lifecycles, like seabirds.

Therefore, we address both the lack of basic ecological knowledge on seabird population abundance and the more complex interactions between species and within the environment for the colony, both during the breeding season, and while at sea.

Research findings

Nest burrowing nocturnal petrels are particularly difficult to study (Buxton et al. 2015; Dyer and Hill 1991; Sutherland and Dann 2012) given their life style. In CHAPTER 2, we explored a new statistical approach to the play-back method, which accounts for imperfect detection of breeding events (present but non-answering birds) during a shearwater census. This method allows a more accurate detection of birds present in the burrows, which are often long, winding and difficult to examine solely by visual survey. The methodology we present in CHAPTER 2 is particularly adequate if the survey is carried out during the peak of the breeding season, when most of the breeding birds are likely to occupy the nests. Unfortunately, in many cases, census surveys have to be performed at a broader timescale for both logistic constraints and the need for a larger sample size (Bibby et al., 2012). In such cases, the pairs that fail to reproduce early are not recorded, as they are no longer present at the breeding grounds. CHAPTER 3 considers this problem using a formula that accounts for both imperfect detection and breeding failure, allowing the census to be carried out on a wider period of time in order to cover a larger sampling area. Once the number of pairs per sampling area is measured, the abundance of both species is assessed using a spatio-temporal model based on habitat selection in order to obtain the abundance and distribution of the two species across the island for three consecutive years. With this study, we confirm that Aride Island is one of the major colonies of tropical shearwater in the world, and apparently the largest known, although lack of data on other colonies prevents us from making a final judgement at this stage on whether or not it is definitively the largest one. However, we also detected a potential decline of this species, which needs to be more deeply investigated. This unexpected finding places the tropical shearwater as a high priority species, both in the context of Aride and also at a wider scale in view of the importance of Aride population in the western Indian Ocean. On Aride, two more seabird species, the roseate tern (*Sterna dougallii*) and the sooty terns (*Onychoprion fuscatus*), are both experiencing a steep decline since the past 20 years (ICS, Aride Island annual reports, unpublished). In contrast, the wedge-tailed shearwater (WTS) population remained stable at about 15 000 pairs. In terms of habitat selection, the two species have a

common preference for steep areas with low vegetation. In addition, the wedge-tailed shearwater selects rocky areas with deep soils, which have been identified as boulder areas (big rocks creating cavities and holding soft soil deposit). It is clear from our study that this species is more selective in terms of habitat compared to the tropical shearwater (TS). Pelagic seabirds such as shearwaters spend most of their life at sea (Guildford et al. 2012; Hedd et al. 2012), on which they depend on for foraging purposes. Therefore, in addition to the important information on what happens at the colony, knowledge about the life cycles stages at sea is fundamental to having a better understanding of the ecology of the species and to identify potential threats, for example when clashes with fishing enterprises occur (Reid et al. 2012). Consequently, information on movements and habitat selection of the individuals at sea becomes an important component of the species conservation actions (Péron et al. 2013). CHAPTER 4 and CHAPTER 5 focus predominantly on the areas exploited by the birds during non-breeding, pre-laying and chick rearing stages, giving important insights on the habitat selection at sea of both species during these crucial stages. In particular, for the first time, CHAPTER 4 describes the TS foraging areas, which are much wider than what was previously speculated in literature (Safford and Hawkins, 2013). They also vary depending on the monsoon seasons that influence the weather in the region, being more dispersed during the North-West than during the South-East monsoon. The movements at sea of the WTS were already known from previous studies (Catry et al. 2009a) and our results only partially reflect such results. This species was confirmed to be highly pelagic with trips covering nearly the whole tropical Indian Ocean. However, in our study, more than half of the tracked birds spent a significant amount of time around Sri Lanka and in the Bay of Bengal, a result which to our knowledge, has never been published before from tracking data. The ecological niche occupied at sea during the breeding season was found to be very similar among the two species while the areas they exploited barely overlapped. This spatial segregation is also perceptible in the results of the diving depth study also presented in CHAPTER 4; the TS maximum diving depth was about 16 m while the WTS didn't show any significant diving activity. The diet of these two species highly overlap (Catry et al. 2009b), therefore this difference in foraging behaviour can be related to competition between the two species in the prey catch process (see more details below). CHAPTER 5 shows the first foraging trips of WTS tracked by GPS, and gives a more detailed insight on the WTS foraging ecology during the early chick rearing for this species in the western Indian Ocean. A well-delimited area (Figure 5.1) was identified as the main foraging ground just beyond the granitic Seychelles bank. This area, along and around the Seychelles continental drop, is characterized by higher primary production compared to surrounding waters. On the contrary, the areas selected during the inter-breeding period were characterized by high temperature, low nutrients concentration and low wind speeds (CHAPTER 4). During chick rearing, especially when the chicks are small, the need to perform frequent visits to the colony forces the parents to find profitable areas relatively close to the breeding ground (Weimerskirch 2007), therefore the choice of foraging in upwelling zones is understandable (CHAPTER 5). During the inter-breeding period the individuals have no longer such constraint and are free to choose the most profitable zones for their self-provisioning before starting a new breeding attempt in the next season (Cherel et al. 2014). However, in the case of the WTS, very poor areas are exploited during the inter-breeding period. Interestingly, very recent studies on the WTS population of Heron Island found the same results, with breeding birds associated to oceanic features,

such as eddies (McDuie et al. 2015) while non-breeding birds select areas with low concentration of nutrients, low wind speed and high temperature (Congdon et al., unpublished). In CHAPTER 4, we hypothesized a strong relationship between both shearwaters and sub-surface predators especially during the interbreeding season; this is based on our habitat selection results and on literature (Thiebot and Weimerskirch 2013, Le Corre et al., 2012). A very recent study (Miller et al., unpublished) on inter-breeding period of WTS in the Pacific modelled sub-surface predators distribution (based on habitat features) finding an overlap between such areas with the areas exploited by the birds. Given that the two populations of WTS (Indian and Pacific Ocean) select the same habitat features during the inter-breeding period, it is very likely that the strong association with sub-surface predators found in the Pacific is also true for the Indian Ocean population. The WTS is therefore associated to local oceanographic features during the breeding seasons (in particular during early chick rearing), while it depends more on associations with sub-surface predators to forage during the inter-breeding period. It is possible that the TS could behave in the same way given the similarity of the two species in terms of prey type (Catry et al. 2009b) and habitat selection at sea. In particular, this species seems to regularly exploit the areas between the Seychelles and the Comoros archipelagos when the productivity in the Western Indian Ocean region is low (North-West monsoon season). This suggests that it could also be strongly associated to sub-surface predators, which are proven to be particularly abundant in that area (Piton and Magnier, 1976). This hypothesis can also be verified by our habitat selection result, since the total tuna catch is one of the main drivers of the TS distribution during the interbreeding and possibly breeding season (see CHAPTER 4).

Interaction and competition among the two species

The study of interspecific competition among two species or within a community can be addressed from a wide variety of approaches: fitness measures (Martin and Martin 2001), population size correlations (Cooper et al. 2007), direct behavioural observations (Human and Gordon 1996; Peck et al. 2014), resource partitioning (Ziv et al. 1993; Martin and Martin, 2001), ecological niche analysis (Pianka 1974; Peers et al. 2013) or habitat distribution (Morris 1989a; Rodriguez 1995), most of which were explored in our study. Our research analysed different life cycle stages of two species of shearwaters that share the same breeding colony. Based on our knowledge, there are very few examples of two shearwaters species so ecologically close to each other, sharing the same colony and breeding partially at the same time (Ramos et al. 1997; Gaze 2000; Navarro et al. 2009). In literature, it is often found that if two shearwater species share the same island they are either segregated in space (Bretagnolle et al. 2000), in time (Monteriro et al. 1996) or in terms of habitat and prey requirements (Catry et al. 2009b; Navarro et al. 2009). On Aride these two species have nearly the same ecological requirements in terms of preys (Catry et al. 2009b), habitat selection in both at the colony (CHAPTER 3) and at sea (CHAPTER 4). When they are not constrained by the breeding season, they undertake different journeys but still select the same habitat, which can be due to the evolutionary history of the two species and might be important in assumptions made about competition. However, many factors can support our hypothesis. For example, we found some difference in the areas exploited by the TS during the inter-breeding season (CHAPTER 4). During the NW

monsoon it tends to leave the Seychelles waters and disperses further. This season also corresponds to the WTS breeding season, meaning that resources consumed by shearwaters could be more available and abundant around the Seychelles waters. Monticelli et al. (2007) showed that two predictable phytoplankton blooms occur each year in the Seychelles area: a small one during the NW monsoon, between December and February, and the main one during the SE monsoon, between May and August (during the breeding season of most seabirds in the area). Therefore, the fact that the TS leaves the area during the NW could be due to better conditions elsewhere but could also be due to a strong competition at sea for foraging fish with its congeneric WTS shearwater. Seabirds' competition at sea for foraging resources has already been proved in tropical waters (Balance et al., 1997) and birds in feeding flocks in the Western Indian Ocean are no exception. If this competition occurs, larger species may be expected to outcompete smaller species via interference competition, simply because the probability of injury from aggressive interactions or collisions with other members of the feeding assemblage increases with decreasing body size (Smith 1990).

The hypothesis of competition can also be supported by the vertical segregation in diving activity found during early chick rearing (CHAPTER 4). Therefore, when the two shearwaters can segregate in space (i. e. at sea), they will do so; however, on land they have no choice but to co-exist as they share almost the same habitat requirements (CHAPTER 3) in the breeding colony. In such cases, the WTS is likely to out-compete the smaller TS. In literature, there are some examples of competition for burrows where the WTS out-competes other co-existing nest burrowing species, for example in New Caledonia it has been proven to be in strong competition for burrows with of the Thaiti petrel (*Pseudobulweria rostrata*), which is also bigger in size compared with the WTS (Villard et al., 2006).

When two species co-exist in the colony, fitness measures, population size correlations and direct behavioural observations can be explored to assess potential competition. The part of our study which explored interactions in the colony showed that the two species share almost the same habitat requirements (CHAPTER 3), even if the WTS was more selective than the TS and the areas with higher density of the two species are situated in different parts of the island (Figure 3.3 in CHAPTER 3). To better examine what is happening in the colony during the breeding seasons we used the data of a long term shearwater nest monitoring program that was started in October 2011 (see APPENDIX I for details). The histograms in figure A.1.1 show in red and green the monthly average of occupied nests by TS and WTS shearwater respectively over a period of three years. The red and the green lines indicate the average failure rate for TS and WTS respectively. The breeding season of the WTS is shown clearly by the occupied nests that start to increase significantly from October and almost completely disappear in April. This is coherent with the phenology of this species. The TS phenology had never been studied in such detail and for a significant length of time before this study. The number of TS occupied nests seem quite constant throughout the year, with small peaks in July and November-December, and a more significant peak in April. The failure rate of this species has a major peak in December (which starts in October and ends in February), and two lower peaks in August and May. The peak of TS breeding in April can be related to the disappearance of the WTS from the colony. Our hypothesis is supported by other studies as the segregation in breeding time due to competition with WTS at the colony was also found in the Bonin petrel (*Pterodroma*

hypoleuca). WTS has been in fact observed to kill or evicted Bonin petrel's chicks in case burrows are shared (Warham 1990). Moreover, in April the oceanographic conditions are not particularly good for seabirds around Seychelles (Monticelli et al., 2007), this could also explain the high TS failure rate the same month.

Moreover, the main peak in TS failure rate starts in correspondence with the beginning of the WTS breeding season and ends exactly at its end, whilst the small failure peak of August may correspond to the arrival of the first WTS at the colony. The major failure peak corresponds to the main period of presence of the WTS on Aride (many young have already fledged in February and pairs previously unsuccessful have already left). These preliminary results indicate a potential strong competition between the two species for breeding grounds, but they need to be analysed in more details.

In addition, out of the 150 nests selected for TS, 30 were successively occupied by WTS and out of the 150 nests selected for WTS, 44 were also occupied by TS (mainly when WTS was not present in the colony). This shows a certain degree of burrows' interchange among species.

From the geolocator recovery rates (CHAPTER 4) and from recaptures of ringed birds (unpublished data), we also observed a much higher partner and nest fidelity of the WTS compared with the TS. This behaviour can also be linked with competition. The hypothesis that inter-specific competition, in addition to environmental and habitat factors, could play a role in the decline of the TS cannot be proved completely. However, we pinpoint an issue previously ignored which could be extremely useful for the conservation of these two species and which would have a significant influence on management aspects.

Conservation and management implications

We have shown that one of the largest populations of TS in the world is apparently declining and that habitat modification in the colony (CHAPTER 3), indirect impacts of intensive fishing and interspecific competition (CHAPTER 4) could play a role in such a decline. Aride Island is a nature reserve, which benefits from the absence of significant human disturbance and in which conservation management actions could be implemented. We previously referred to management debates on nature reserves and how human intervention in an integral reserve can be discouraged in favour for "leaving the nature to take its course" (CHAPTER 1). On Aride, if a non-intervention policy is undertaken, the risk of forever losing certain species is a reality (e.g. the endangered Seychelles magpie robin, or the rare roseate tern). In this study we focus in particular on shearwaters, but other seabird populations are also experiencing serious declines. For example, despite yearly fluctuations, the sooty tern went clearly down from 300 000 to 35 000 pairs and the roseate tern (both species reaching thresholds of international importance) from 3 000 to 300 breeding pairs in approximately two decades (Rocamora & Skerrett 2001; Bowler et al., 2001; Aride Island Annual reports, unpublished).

The causes of such declines are still little understood, but could include habitat modification, over-fishing and climate change (Monticelli et al. 2014; Pedro et al. 2014). In regards to over-fishing and climate change, there is little a single nature reserve manager can do short of joining a stronger and well organized conservationist lobby (Chu 2009; Wright 2000). However, the habitat in the nature reserve can be modified to optimize the breeding conditions of the species that requires particular help. In CHAPTER 3 some habitat

intervention in favour of the TS has been suggested, which mainly involves reducing patches of tall *Pisonia grandis* forest in areas particularly favourable for the species. This is especially the case in steep areas with low soil depth, to discourage the WTS to dominate the areas. In the Pacific islands, the WTS breeding sites are often associated with vegetation, in particular with *Pisonia* trees, because this plant species grows at an exceptional rate and its big roots act as soil stabilizers (Congdon, personal comment). If patches of *Pisonia* are removed in areas favourable for the TS with low soil depth and absence of boulders, the WTS might be discouraged to breed in such areas even if low vegetation and high slope may act as attracting factors. This could reduce the spatial competition between the two species in the colony. Opening glades can also benefit the roseate and the sooty tern; in fact their decline seemed to happen together with the progressive and fast island spontaneous reforestation (Calabrese and Maggs, annual report 2013).

In practical terms, despite the high public interest in the environment in many parts of the world, conservationists and non-profit organizations are generally very short of funds. It is therefore essential to direct the available money towards species or habitats where it will do the most good (Hamblen 2004). Aride Island, as with many nature reserves in developing countries, runs on a very low budget. However, the presence of permanent staff and volunteers on the island could make the vegetation management a relatively cheap task. The biggest problem in that regard could be the continuous work of maintenance that the glades will require to remain open; in absence of other tree species to act as competitors, the fast growing *Pisonia* would take very little time to recolonize the newly cleared glades. This maintenance of long term glades could be avoided if at the edge of the glades (or even inside) small shrub tree species are planted. For example, the species *Morinda citrifolia* is a slow growing and small tree native of Seychelles. If planted in the cleared glades, thanks to the provided shade it could prevent the *Pisonia* to take over. In fact, it has been observed that some native trees, including *Morinda*, can progressively reduce the cover of *Pisonia* (Rocamora and Calabrese personal observation).

This tree remains relatively short (< 5-6 m), therefore presumably it won't have any negative impact on the TS (as shown in CHAPTER 3, the TS selects vegetation < 5 m). Previous studies have shown that the prevalence of roseate terns can be facilitated by small vegetation shading in the colony (Ramos et al. 2007). Opening more glades around the colony and planting *Morinda citrifolia* could therefore help their reproduction too.

In areas where TS and WTS coexist in high density, clearing the vegetation might have different results. Therefore, in these areas, the option of using artificial shearwaters nest boxes could be investigated. Additionally, the entrance to the boxes could be adapted to only admit birds the size of the TS, hence preventing the WTS from exploiting the same nest. Artificial burrows have already been used with success in many Pacific island and studies from across the world found evidence for population increases or new populations being established in petrel species following the provision of nest boxes (Bolton et al., 2004; Priddel et al., 2006). However, we have no examples of how the vegetation management we propose can help the TS and the roseate tern populations to recover. Therefore, before planning a large scale intervention, a small scale trial of habitat management is required to produce conservation evidences (Sutherland 2004). Given shearwaters' longevity, the effect of such trial will require some years to be ascertained. It is therefore important to monitor the population constantly to observe any positive or negative outcomes from this vegetation trial.

To conclude, like previous studies, we hypothesize a strong association between sub-surface predators and shearwaters, thus highlighting the importance of establishing an appropriate management scheme to prevent the over-fishing of key stock of tuna fish. Overfishing can become an indirect threat for this shearwater population, as it can lead to a decrement in the foraging fish available.

We propose here the undertaking of a habitat management trial, but unlike most of conservation studies we don't suggest the removal of alien invasive species to restore a lost ecosystem, but to control a native tree species which has become widespread due to anthropogenic habitat modification (see CHAPTER 1 and CHAPTER 3). Potentially, these actions could help to rebuild shearwater species numbers on Aride. However, if more islands are made suitable for shearwater breeding through the eradication of alien predators (Rocamora & Henriette, in press), this could create more breeding grounds for the species and therefore relieve competition between them for the few available breeding sites.

APPENDIX I

Breeding success analysis of tropical shearwater and wedge-tailed shearwater populations on Aride Island.

Materials and Methods

With the aim of assessing the breeding success of wedge-tailed (WTS) and tropical (TS) shearwater on Aride Island, we marked and regularly checked a number of burrows for both species.

In October 2011, 160 burrows (100 for the wedge-tailed and 60 for the tropical shearwaters) were selected at night in six different areas of the island. From August 2012, more nests were selected to increment the sample size (as the actual number of occupied burrows resulted to be too low for the TS). A sample size of 300 monitored burrows was reached by the end of 2013 (150 selected as TS and 150 as WTS burrows). For the first year of study burrows were monitored weekly, and afterwards, every 2 weeks. The burrows were selected at night preferentially at pair stage (i.e. the pair is present inside the burrow). There are cases where a burrow was selected at egg or chick stage, these burrows were removed from the analysis for the season in which they were found but were kept monitored and considered in the calculation of the breeding success of the following breeding event. For this study, the data from October 2011 to October 2014 were considered, hence a total duration of over three complete years for the study. The nest check is still on going and became part of the island monitoring program.

The average percentage of occupied nests (containing either a pair, an egg or a chick) and the average failure rate per month was calculated per each species over the three years period.

Results

Figure A1.1 shows the average percentage of occupied burrows and the average failure rate per month and for each species over the three consecutive years. The seasonality of the WTS is obvious with a peak of occupancy in October and November, which also correspond to two peaks of failure rate in November (egg stage) and January (small chick stage). The results for the TS confirms it as year-round breeder, with two minor peaks in July and November/December, and one main peak in April. The failure rate also presents three peaks, of which the main one is in December/January, shortly after the TS peak of breeding season.

In addition, out of the 150 nests selected for TS, 30 were successively occupied by WTS and out of the 150 nests selected for WTS, 44 were also occupied by TS, mainly when WTS was not present in the colony. This shows a certain degree of interchangeability of burrows among species.

These results are discussed in the general discussion (CHAPTER 6).

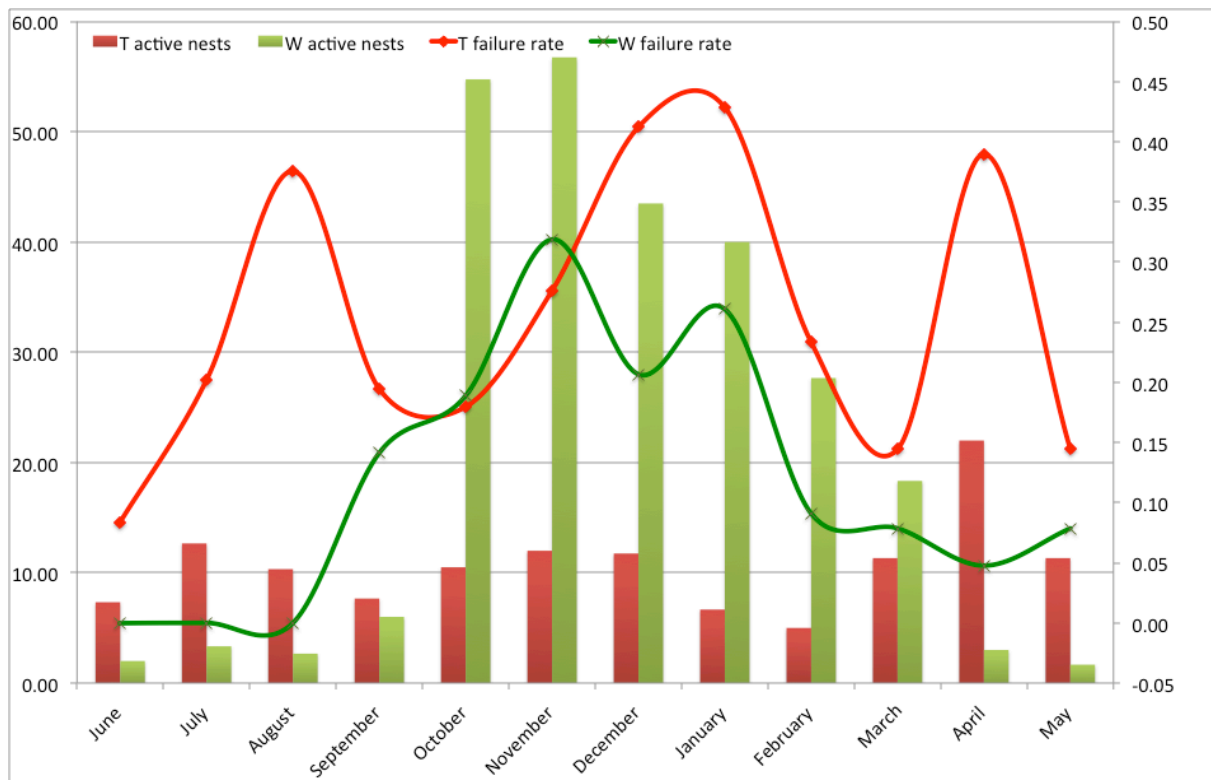


Figure A1.1. Average percentage of occupied burrows (histograms and left y axis) and failure rate (lines and right y axis) of tropical (T) and wedge-tailed (W) shearwaters.

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