Eduardo Castro Lobato

Driven by the moon: the foraging behaviour of Procellariiforms at night

Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia, realizada sob a orientação científica do Doutor Vítor Hugo Rodrigues Paiva (Universidade de Coimbra) e do Professor Doutor Jaime Albino Ramos (Universidade de Coimbra)

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UNIVERSIDADE DE COIMBRA

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Abstract

Procellariiforms are almost exclusively pelagic marine predators, with some species exhibiting a predominately nocturnal foraging activity. The main objective of this thesis was to investigate the effect of the moonlight on three different sized procellariiform seabirds - Cory's Shearwater, *Calonectris borealis*, Deserta Petrel, *Pterodroma deserta* and Macaronesian shearwaters, *Puffinus baroli,* breeding at Berlenga Island (mainland Portugal), Bugio (Madeira archipelago) and Cima and Selvagem Grande Islets (Madeira archipelago), respectively, during the breeding seasons of 2007-2017. Global Location Sensing (GLS) devices were mounted on the birds' tarsus and location and activity data was then filtered to analyse the nocturnal foraging activity of the individuals during their breeding and non-breeding periods. Such individual tracking data was then used to investigate the effect of moonlight (full and new moon and quarters) on the (1) at-sea behaviour, (2) colony attendance while breeding and (3) migratory schedule.

Overall our results indicate that the moon influenced these seabirds in the former three behaviours. Under full moonlight small sized procellariiforms (Macaronesian shearwaters and Desertas petrels) increased their at sea activity (e.g. more time spent flying), foraged in more pelagic, high depth and windier domains, decreased their colony attendance when compared to a larger sized procellariform (Cory's shearwater). Full moon also dictated a higher number of departures in pre- and post-breeding migrations for the transequatorial migrants (Cory's shearwaters and Desertas petrels) but not for the resident species (Macaronesian shearwater).

Resumo

Os procellariiformes são aves marinhas predadoras, quase exclusivamente pelágicas, que em algumas espécies exibem atividade predominantemente noturna na alimentação e na procura de presas (atividade no mar). O principal objetivo desta tese foi investigar o efeito da lua em três aves procellariiformes de diferentes tamanhos - cagarra, *Calonectris borealis*, freira-do-bugio, *Pterodroma deserta* e o pintaínho, *Puffinus baroli*, que se reproduzem na Ilha das Berlengas (Portugal), Ilha do Bugio (Arquipélago da Madeira) e Ilhéu de Cima e Selvagem Grande (arquipélago da Madeira), respetivamente, durante os anos de 2007-2017. Foram colocados no tarso destas aves, dispositivos *Global Location Sensing (GLS)*. Estes dispositivos permitem saber a localização e obter dados sobre a atividade, sobre a forma de luminosidade e salinidade, das aves. Posteriormente, os dados de atividade foram filtrados de forma a permitir analisar a atividade noturna dos indivíduos durante seus períodos de reprodução e fora da reprodução. Os dados obtidos foram então utilizados para investigar o efeito da lua (lua cheia, nova e quartos) no (1) comportamento no mar, (2) nas visitas a colónia durante a época de reprodução e (3) nos movimentos migratórios.

Globalmente, os nossos resultados indicam que a lua influenciou essas aves marinhas nos três comportamentos descritos anteriormente. Sob períodos de lua cheia as espécies de pequeno porte, a freira-do-bugio e o pintaínho, aumentaram a sua atividade no mar (por exemplo, mais tempo gasto a voar), procuraram alimento em zonas mais pelágicas, de alta profundidade e com mais vento, e também diminuíram o numero de visitas à colónia quando comparados com um procellariiforme de maior porte (cagarra). A Lua cheia também ditou um maior número de partidas em migrações pré- e pós- época de reprodução para os migrantes transequatoriais (cagarra e freira-do-bugio), mas não para a espécie residente (pintaínho).

Palavras-chave: Ciclo da lua, Lua, Atividade no mar, Visitas a colónia, Movimentos Migratórios, *Calonectris borealis***,** *Pterodroma deserta***,** *Puffinus baroli*

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Chapter I - Introduction

1.1 Marine environment and Marine top predators

Marine environments are among the largest, most varied and complex ecosystems on Earth (Verity et al., 2002) linking multiple scales by flow of water and species movements (Levin & Lubchenco, 2008). Marine productivity tends to be heterogeneously distributed, with high productive areas located close to specific areas such as shelf edges or coastal upwellings (Ainley & Boekelheide, 1990; Bakun, 1990; Crawford, 2007). Ocean currents, winds or river influx introduce varying complexities in the interlinkages between biotic components and environmental characteristics especially in coastal waters (Chen et al., 2004; Wetz & Wheeler 2004; Tweddle et al., 2010). For example in wind-driven coastal upwelling there is the rise of cold and deep subsurface waters that are rich in nutrients, and will contribute for an increase in the density of primary producers such as phytoplankton, which will consequentially attract zooplankton, followed by pelagic fish , and then top predators such as large fish, cetaceans or seabirds (Malik et al., 2015). It is well known that cephalopods (Nakamura et al., 1993) and mesopelagic fish (Gjøsaeter & Kawaguchi, 1980) are preyed by procellariiforms, because some make a diel vertical migration making them available to shallow divers during darkness (Roper & Young, 1975; Gjøsaeter & Kawaguchi, 1980; Harrison et al., 1983; McLintock, 2007). Marine top predators are thus dependent of lower trophic levels, and their ecology is mostly influenced by what happens at those lower trophic levels, known as a 'bottom-up' effect. Therefore, marine top predators are good sentinels of changes in marine ecosystems, and their population trends and ecology may be used to understand and manage marine ecosystems. Among the marine top predators, seabirds are considered very good bioindicators of the marine ecosystem, because of their wide at-sea distribution and the easiness to handle and track them at their colonies. But also, because unexpected changes in their numbers, health or breeding success can provide an alarm that may indicate an unknown pollution or food supply problem (Furness & Camphuysen, 1997).

1.2 The influence of the moon on the life cycle on marine organisms

In the vast ocean, there are a great number of organisms that depend on each other to survive (Verity et al., 2002). However, behaviours and interactions are often associated with certain abiotic characteristics such as the moon. Therefore, studies on the effects of lunar cycle on the behavioural patterns of marine organism have been relatively common, and we include here some characteristic findings: a) in four species of *Pocillipora (P. damicornis P. eydouxi, P. verrucosa* and *P. meandrina)* spawning occurs 1–2 days following the full moon (Schmidt-

Roach et al., 2012), b) for Bermuda fireworm (*Odontosyllis enopla*) the breeding is thought to be a response to the lunar cycle of illumination (Korringa, 1957), c) in the California grunion (*Leuresthes tenuis*) the spawning only occurs three or four nights after full or new moon (Walker, 1952), d) some mesopelagic fish and cephalopods species (eg. *Selenoteuthis scintillans; Abraliopsis sp.; Pyroteuthis margaritifera*) typically perform diel vertical migrations (DVM) in the darkness (Roper & Young, 1975; Gjøsaeter & Kawaguchi, 1980; Harrison et al., 1983; McLintock, 2007), f) also some seabird species exploit these vertical migrations of cephalopods and mesopelagic prey to feed themselves, and therefore benefit indirectly from the influence of the moon (Dias et al., 2012b). Therefore, the moon/darkness affects many marine species and the prey-predator relationships. It is known that certain prey species they tend to become less active (Clarke, 1983; Sábato et al., 2006; Berger-Tal et al., 2010) around full moon periods. Thus, it is expected that nocturnal predators increase their activity during nights with more light intensity, because under those conditions they can opportunistically take advantages of the higher illumination and use it to find their prey (Clarke 1983; Kotler et al., 1988; Penteriani, 2011).

The most obvious influence the moon can exert on the marine environment is modulating light intensity, so some species are more liable to exploit the moonlight effect, a higher luminosity, and thus associate their movement patterns and their behaviours to the 29.2 days' moon cycle. This type of behaviours can be: (a) a response to lunar stimuli (moonlight) (e.g. Mougeot & Bretagnolle 2000; Pinet et al., 2011) or (b) an adaptation of their rhythmic activity to the long-term cycles, being reproducible through time because of their "biological clock" (endogenous cycles) (Mougeot & Bretagnolle 2000). Still, many details of the moon's effects on marine organisms' behaviour remain largely unknown, and more research is needed to explore the effects of the moon on the behaviour of marine organisms.

1.3 The influence of moonlight on the behaviour of pelagic seabirds

Pelagic seabirds spend most of their time in the ocean, and only during the breeding season they visit their colonies, some of them in remote islands, to reproduce. Most procellariiformes forage only in the upper few meters (0 - 5m) of the water column but some species can dive deeper (Taylor, 2008). The occurrence of several oceanographic phenomena and physical features allow to concentrate prey in the upper meters of the water column, which is particularly evident during upwelling events, when there is an increase of the concentration of nutrients in top levels of the ocean, and thus an increase in the amount of species at the

surface (Mann & Lazier 2006, Sherman & Hempel 2009). Therefore, seabirds that are known to feed mostly on crustaceans, cephalopods, and fish (Paiva et al., 2010; Ramírez et al., 2013; Ramos et al., 2015;) can exploit these oceanographic phenomena, increasing their foraging success (Mann & Lazier 2006; Grémillet et al., 2008; Ramírez et al., 2013).

Some seabirds are predominantly nocturnal (Brooke & Prince 1991), in particular those of the order Procellariiformes (Bourgeois et al., 2008; Riou & Hamer 2008; Dias et al., 2012b, Ramirez et al., 2013; Dias et al., 2015). Given their nocturnal behaviour, some studies related the effect of the moon in the activity rhythms of these seabird species. Seabird species such as the Blue Petrel (*Halobaena caerulea*), Thin-billed Prion (*Pachyptila belcheri*) *and* Common Diving Petrel (*Pelecanoides urinatrix*) decrease their activity with higher moon luminosity at night, which could be an effective way to reduce the "predation risk" (Mougeot & Bretagnolle 2000). Several species like the Barau's Petrel (*Pterodroma baraui*) (Pinet et al., 2012), the Scopoli's Shearwater (*Calonectris diomedea*) (Rubolini et al., 2014) and Cory's shearwater (*Calonectris borealis*) (Dias et al., 2012b) spend more time flying during full moon periods increasing their foraging effort, which can be explained by the influence of the moon cycle on the availability of mesopelagic prey species at the surface (Roper & Young, 1975; Gjøsaeter & Kawaguchi, 1980; Harrison et al., 1983; McLintock, 2007), and the increase visibility provided by the moonlight, which allows these species to increase their forage effort (Pinet et al., 2011; Dias et al., 2012b;). The moonlight levels did not influence the at-sea night-time activity of other species such as the Bulwer's petrel (*Bulweria bulwerii*), however this species is a highly specialized nocturnal seabird well adapted to locate and capture prey during the night (Dias et al., 2015). It is also known that during the ''stationary'' stages of migration (wintering and stopovers), when outside the stopovers, Cory's shearwaters, more than doubled the time spent flying during darkness (Dias et al., 2012a), which can be explained by the need to "refuel" as fast as possible to return to the migration movement.

So, it is normal to assume the moon affects the behaviour of pelagic seabirds, and possibly in 3 different phases of their annual cycle: at-sea, at the colony and during migration.

1.3.1 At sea Behaviour

Foraging strategies of top predators such as seabirds are strongly influenced by spatial and temporal fluctuations in prey availability (Paiva et al., 2013). It is already known that the moon affect the at-sea behaviour of procellariforms, for example in Barau's petrel (Pinet et al., 2011); White-chinned petrel (*Procellaria aequinoctialis*) (Mackley et al., 2011), Yelkouan

Shearwater (*Puffinus yelkouan*) (Bourgeois et al., 2008), Cory's Shearwater (Dias et al., 2012b), Streaked Shearwater (*Calonectris leucomelas*) (Yamamoto et al., 2008); Bugio petrels or Desertas petrel (*Pterodroma deserta*) (Ramirez et al., 2013) Scopoli's Shearwater (Rubolini et al., 2014), Fea's petrel (*Pterodroma feae*) and Zino's Petrel (*Pterodroma madeira*) (Ramos et al., 2016) increasing their activity during nights of higher illumination and showing some sort of relation with the lunar cycle. These cases can probably be explained by (1) higher visibility, higher activity searching for prey and a lower use of the "sit and wait" strategy, or (2) lack of food resources, because some prey avoid the full moon because they are more exposed to predators (Ramírez et al., 2013). However, is not clearly why and how the moon is associated with these effects, and if the size/diet of the bird is an important variable to explain these types of behaviours.

1.3.2 Colony attendance

Seabirds usually gather in large and dense colonies to breed, and the number of birds visiting the colonies vary widely, but in some species, there are very clear cycles (Granadeiro et al., 2009). It is known that some colonial seabirds arrive on the colony around a full moon period (Pinet et al., 2011), so colonial Procellariiformes are expected to synchronize attendance at the colonies with the moon phase.

The Procellariforms are known to attend the colonies, in the breeding season, mostly at night (del Hoyo et al., 1992) and there are many studies that suggest these seabirds avoid moonlight when arriving at the colonies; such as the Leach's Storm-Petrels (*Oceanodroma leucorhoa*) (Watanuki, 1986); Blue Petrel, Thin-billed Prion Common Diving-petrel and White-headed Petrel (*Pterodroma lessonii*) (Mougeot & Bretagnolle, 2000); Black-vented Shearwaters (*Puffinus opisthomelas*) (Keitt et al., 2004); Manx shearwaters (*Puffinus puffinus*) (Riou & Hamer, 2008) and Scopoli's shearwaters (Rubolini et al., 2014). Interestingly, in large colonies of Cory's Shearwater, the birds are apparently not influenced by the lunar cycle, and instead follow a biological endogenous cycle (Granadeiro et al., 2009).

Once at the colony some species reduce their vocal activity (e.g. Blue Petrel, Thin-billed Prion and Common Diving-petrel) under moonlight conditions, but the White-headed Petrel was influenced by the lunar phase rather than by an increase in the moonlight level (Mougeot & Bretagnolle 2000). It is also known that Scopoli's Shearwater wait for moments of darkness to enter the burrows under moonless conditions (Rubolini et al., 2014). These types of behaviours have in common the moonlight or the moon itself, and mostly can be explained

by some sort of predation risk avoidance, and thus contributing to increase the survival rate of the birds (Jones et al., 1989; Shealer & Kress 1991; del Hoyo et al., 1992; Mougeot & Bretagnolle 2000;).

1.3.3 Migration Movements

The long-distance migrations carried out by many animals every year are at the expense of considerable costs in terms of time, energy and, in some cases, predation risk. So, it is expected that long-distance migrant seabirds minimize the time of the migratory journey (Dias et al., 2012a) and consequentially decreasing the energy cost of these movements. Seabirds are known to decrease their migration time by foraging while they are travelling, opting for a fly and forage strategy (Strandberg & Alerstam, 2007) but sometimes they need to stop, usually in the most favourable spots and accumulate enough body reserves to complete the trip (Alerstam & Lindstrom, 1990).

Some seabirds are known to make this stopover's during their migratory journeys for example the Manx shearwaters (Guilford et al., 2009), Cory's shearwaters (Dias et al., 2011) Arctic terns (*Sterna paradisaea*) (Egevang et al., 2010), long-tailed skuas (*Stercorarius longicaudus*) (Sittler et al., 2011), South Polar skuas (*Catharacta maccormicki*) (Kopp et al., 2011). In the case of the Cory's shearwater, some individuals can make the return migration without making any stopovers, without showing any pre-fattening, thus suggesting that these seabirds can make hundreds of kilometres without stooping for long periods (Dias et al., 2012a).

Also, some pelagic migrant's seabirds are often faithful to their wintering sites in successive years, such as the Cory's Shearwater (Dias et al., 2011), Yelkouan shearwater (Raine et al., 2013), Grey-headed albatrosses (*Thalassarche chrysostoma*) (Croxall et al., 2005) and Northern Fulmar (*Fulmarus glacialis*) (Hatch et al., 2010). It is also known that procellariforms have some sort of constancy on the dates of departure and arrival dates on the colony, such as the case of the Cory's Shearwater (Dias et al., 2011). In Barau's Petrel the mean arrivals dates to the colonies coincided with the full moon (Pinet et al., 2011). Also, the moon phase affected the arrival date at the colony after the pre-breeding migration in Sooty terns (*Onychoprion fuscatus*) (Chapin et al., 1959).

Phalan et al., (2007) suggested that during full moon nights birds can use visual cues to pursue their prey from the air. An increase in flight activity during moonlit nights was registered in several other seabirds outside the migration periods, for example for Waved

albatross (*Phoebastria irrorata*) (Awkerman et al., 2005) Streaked Shearwater (Yamamoto et al., 2008) and White-chinned petrel (Mackley et al., 2011). In migration, Cory's shearwaters flew significantly more during darkness and less during daylight, and have a flight activity peak around dusk (Dias et al., 2012a).

Therefore, it is assumed that Procellariiformes while migrating, should increase their flight time during moonlight nights, possibly exploring the increase of visibility (Rubolini et al., 2014). However, few studies have addressed the effect of moonlight on migration timing and routes, and on arrival in stopovers and the actual location and role of these stopovers.

1.4 Thesis objectives

In this study, our main goal is to evaluate "How the moonlight affect the behaviour of Procellariiform seabirds". To do so we sub-divided their moon-related behaviour in 3 parts (1) at sea, (2) Colony Attendance and (3) on Migratory Schedule. To evaluate the effect of moonlight on the behaviour of procellariforms we selected three procellariiform seabirds: the Macaronesian shearwater (*Puffinus baroli*), Deserta's petrel (*Pterodroma deserta*) and Cory's shearwater (*Calonectris borealis*). These three species differ mostly in body size, with Macaronesian shearwaters being a small-sized (~160 gr in body mass), Deserta's petrel a medium-sized (~320gr) and Cory's shearwater a big-sized (~800gr) seabird species. These three species also differ in the proportion of cephalopods in their diet, with Macaronesian shearwaters having a diet composition with 60% of cephalopods (Ramos et al., 2015), Deserta's petrels with 40%-50% (Ramírez et al., 2013) and Cory's shearwaters with 10%-20% of cephalopods (Paiva et al., 2010).

We addressed the following questions (1) "Is the at-sea behaviour of the three-species similar in relation to the different phases of the moon cycle?" (2) "Do the three species adopt different colony attendance patterns in relation to the phase of the moon cycles?" (3) "Does the timing of migration vary among the three species according to the moon cycle?"

In this study, at-sea we expect that these three-procellariform species will generally increase their activity at night, with a significantly higher activity on full moon nights. This is expected because many other procellariforms already studied (Barau's petrel (Pinet et al., 2011); White-chinned petrel (Mackley et al., 2011), Yelkouan Shearwater (Bourgeois et al., 2008), Cory's Shearwater (Dias et al., 2012b), Streaked Shearwater (Yamamoto et al., 2008); Deserta's petrels (Ramirez et al., 2013) Scopoli's Shearwater (Rubolini et al., 2014), Fea's petrel and Zino's Petrel (Ramos et al., 2016) also increase their at-sea activity during the nights

of higher illumination. This increase of activity, on the aforementioned species, has been mainly explained by two hypothesis (1) the full moon increases visibility so they tend to take this advantage to try find prey and (2) with the increase in moonlight, prey tend to hide more, therefore full moon may present a negative correlation with prey abundance, and this may lead this species to increase their "foraging effort". We also expect an even higher activity of *Puffinus baroli* at night, when there is a higher number of the favourite prey, cephalopods, at the surface of the ocean.

In relation to the *Deserta's petrel* and *Cory's shearwater* it is known that they spend more time flying during moonlight nights (Dias et al., 2012b; Ramírez et al., 2013). Overall, we expect all three study species to increase their at-sea activity and foraging effort during full moon days (Dias et al., 2012b; Ramírez et al., 2013; Paiva et al., 2016) and during the breeding phase, possibly because of the higher energetic demands of chick-provisioning.

In relation to colony attendance, it has been reported that some seabirds wait for moonlit nights to return to their colony (e.g. Leach's storm-Petrel (Watanuki, 1986); Blue Petrel, Thin-billed Prion, Common diving-petrel, White-headed Petrel (Mougeot & Bretagnolle, 2000); Black-vented shearwaters (Keitt et al., 2004); Manx shearwaters (Riou & Hamer, 2008) Scopoli's shearwaters (Rubolini et al., 2014). We expected Desertas Petrel and Macaronesian shearwater to be more influenced by the moon cycle when visiting the colony, because the colony attendance of other Procellariforms of similar size (eg. White-headed Petrel (*Pterodroma lessonii*) Manx shearwaters (*Puffinus puffinus*)) were influenced by the moonlight, justified by (1) some sort of predation pressure or (2) by an endogenous cycle. Therefore, if the avoidance of moonlight is driven by predation risk, the size of the species will be an important factor in explaining colony attendance patterns in relation with moonlight (Mougeot & Bretagnolle 2000). Larger species (*Calonectis borealis*) will be less affected by the moon light than smaller species (*Pterodroma deserta* and *Puffinus baroli*).

In terms of migration, Cory's shearwater and Desertas petrel are trans-equatorial migratory birds (Dias et al., 2012a; Ramírez et al., 2013) whereas the Macaronesian shearwater is a relatively sedentary species (Ramos et al., 2015). We intend to know if the trans-equatorial migratory birds will synchronize their journeys the with the moon cycle, in order to minimize the energy and time cost of long-distance migrations. So, we expect the departures in pre- and post- breeding migrations of the trans-equatorial migratory species to coincide around the full moon period, because can provide better conditions, for example a higher illumination, to pursue prey (Phalan et al., 2007), and therefore to minimize the timing spent in stopovers to refuel and complete these long-distance movements.

Chapter II - Methods

Luís Ferreira

2.1 Fieldwork and tracking

Between 2007–2017, global location sensing (GLS) loggers were deployed and recovered from Cory's shearwaters (N = 28, between 2011-2017), Deserta Petrel (N = 54, between 2007-2015) and Macaronesian shearwaters (N = 23, between 2011-2015) breeding at Berlenga Island (mainland Portugal), Bugio (Madeira archipelago) and Cima and Selvagem Grande Islets (Madeira archipelago), respectively.

Devices were attached with a cable-tie to the ring at the bird tarsus, and provided recorded light (for geolocation) and salt-water immersion (for analysis of activity) data. The geolocation is the calculation of position (twice per day) from ambient light level readings regarding time. Latitude and longitude were estimated from day (night) length and the time of local noon (mid-night), respectively, in relation to Greenwich time (Phillips et al., 2004).

Geolocator devices represented 1.5%; 0.5–0.9%; ~0.3 % of the individuals' body mass, respectively for Macaronesian shearwater, Desertas petrel and Cory's shearwater. This, i.e. a value < 3%, is believed to have no deleterious effects on the foraging distribution and at-sea behaviour of seabird species on the birds' activities (Phillips et al., 2003; Igual et al., 2005). These three species were previously tracked with geolocators without any reported negative effect (Neves et al., 2012; Missagia et al., 2015; Ramos et al., 2015; Fagundes et al., 2016; Paiva et al., 2016; Ramos et al., 2016).

Data were analysed using the BASTrack software suite (British Antarctic Survey, Cambridge, UK), using a light threshold of 10 and with elevation angles of -4.5, -4.0 and -4.0 (derived from calibration devices left at Selvagem Grande, Berlengas and Porto Santo, respectively). On quality of the light curves checked with TransEdit we observed they were high, so the geolocation error should be similar to the estimated by Phillips et al., 2004. We removed location derived from curves with apparent interruptions around sun-set and sunrise and impossible locations checked around equinoxes were also excluded.

Because we were interested in analysing the moon effect on the foraging activity of our study species, for further analysis we only used the data for the night period. This was defined as the period between dawn and sunshine, from inspecting the light data of each individual geolocator.

2.2 At-sea activity

The activity patterns of these seabirds were derived from both light level data recorded and immersion for each individual of each species. The loggers have two electrodes that record the salt-water immersion every three second using and stored the number of positive tests at the end of each 10 min period from 0 (continuously dry) to 200 (continuously wet).

The immersion data were categorized into day and night (based on the light data) representing the proportion of time spent on the sea surface (as distinct from flying or on land) during day and night.

The loggers also measured light level every minute and stored the maximum (value of 64) at the end of each 10 min period. Each 10 min block was categorized as daylight or darkness, based on the timing of nautical twilight (derived by interpreting light curves in TransEdit; BASTrack software) following Mackley et al., 2010. Is important to refer that was excluded periods spent in burrows (prolonged periods of darkness and dry record at day time more than 40 min). Periods that the birds spent on the water surface were identified as any continuous sequence of 10 min blocks with at least 3 s sitting on the water, while a continuous sequence of dry (0) values was considered as a flight bout.

Light and activity (immersion) data were used simultaneously to distinguish time spent at sea from time in the colony (burrows) and hence colony attendance patterns. These patterns and the duration of foraging trips, identified based on the logger data, were sometimes confirmed on the ground by monitoring the burrow visits of the tracked individuals.

We considered two different periods as major phases of the yearly life cycle of each of the species, which were used as units of analysis throughout the work: (1) the breeding (Cory's shearwaters - April-October (Missagia et al., 2015); Desertas petrel - June-November (Ramirez et al., 2013) Macaronesian shearwater - December–May (Ramos et al., 2015) and (2) the non-breeding (Cory's shearwaters - November-May (Missagia et al., 2015); Desertas petrel - December-April (Ramos et al., 2016) Macaronesian shearwater – June - November (Ramos et al., 2015) periods. These periods were identified checking both location and the light (*.lig) and activity (*.act) datasets within R (i.e. mainly using several functions of *adehabitatHR* package; Calenge, 2006).

2.3 Environmental characteristics of at-sea habitats used

To define the oceanographic conditions in areas used by the tracked individuals we extracted: (1) Bathymetry (BAT, blended ETOPO1 product, 0.01° spatial resolution, m), (2) Sea Surface Temperature (SST, Aqua MODIS NPP, 0.04°, °C), (3) sea surface Chlorophyll *a* concentration (CHL, Aqua MODIS NPP, 0.04°, mgm^{-3}) and (4) wind speed (WSPD, QuickSCAT, 0.12°, ms^{-1}). Variables (1-3) were downloaded from the BloomWatch website (http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp), while WSPD was extracted from the SeaWinds database (http://winds.jpl.nasa.gov). Monthly averages were used for the dynamic variables (variables 2-4). All environmental predictors were gathered to the coarsest grid cell (0.25°). This is more accurate than the geolocation data, which have an error of c. 180 km (Phillips et al., 2004).

The fraction of the moon illuminated at midnight was obtained for each day from the United States Naval Meteorology and Oceanography Command (http://aa.usno.navy.mil/faq/docs/moon_phases.php). The data were grouped in three phases: new moon (less than 30% of moon illuminated), quarters (30–70% of illuminated moon) and full moon (more than 70% of illuminated moon).

2.4 Statistical analysis

Generalized Linear Mixed Models (GLMMs; *lme4* package; Bates et al., 2013) tested the effect of the interaction between species (Cory's shearwater, Desertas petrel and Macaronesian shearwater) and moon phase (new, quarter and full moon) on foraging parameters (% time flying during the night, % landings, % number of colony visits, max. dist. to colony, % departures for pre- and post-breeding migrations) and characteristics of habitats used (sea depth, SST, Chlorophyll *a* concentration and wind speed) by the former three seabird species during their breeding and non-breeding periods. The individual was used as a random effect to avoid pseudo-replication issues. Effect was evaluated with post-hoc multiple comparisons with Bonferroni correction.

All variables were visually examined for normality (using Q-Q plots) and homoscedasticity (using Cleveland dotplots) before each statistical test, and arc-sine transformed (% time flying during the night, % landings, % number of colony visits, % departures for pre- and post-breeding migrations) when necessary. All statistical analyses were performed using the software R. Results are given as means (± 1 SD) with a significance level at $p < 0.05$.

Chapter III – Results

madeirabirds.com
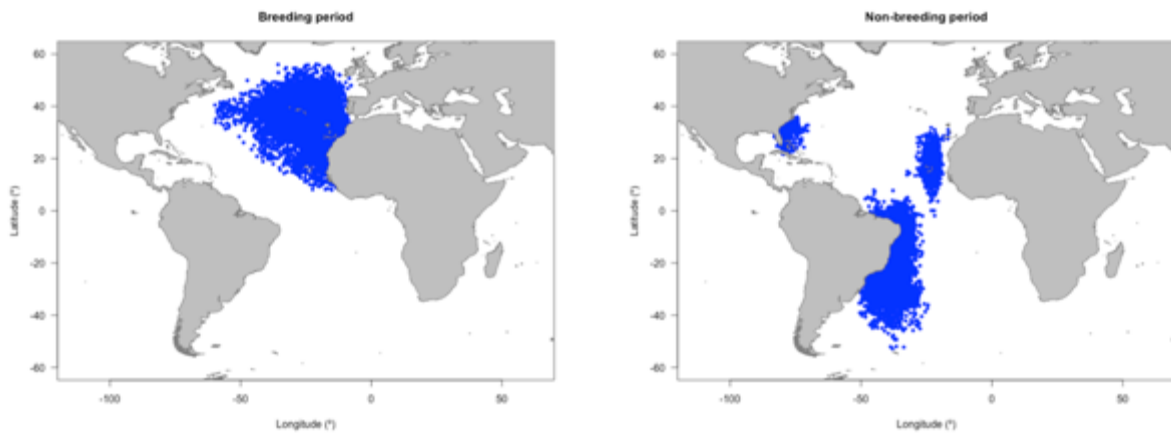
3.1 At-sea distribution

During the breeding phase all seabird species concentrated their foraging activities on their colony surroundings, with Desertas petrels exhibiting a wider distribution when compared to Cory's and Macaronesian shearwaters (Fig. 1).

When relieved from their breeding duties, Cory's shearwaters dispersed from their breeding grounds to spend the non-breeding period (1) at the North Atlantic, off Canada, (2) off West Africa, (3) off South Africa, (4) Off South Brazil and (5) in a pelagic region of South Atlantic (Annex 1). Desertas petrels concentrated their non-breeding foraging activity (1) at the coast of the United States of America, (2) within the Cabo Verde archipelago, off (3) North and (4) South Brazil and (5) in a pelagic region of South Atlantic (Annex 2). Macaronesian shearwater dispersed to the North Atlantic, off Azores, never incurring on a transequatorial migration (Annex 3; Fig. 1).

(A) Cory's shearwater (N = 28; between 2011 2017)
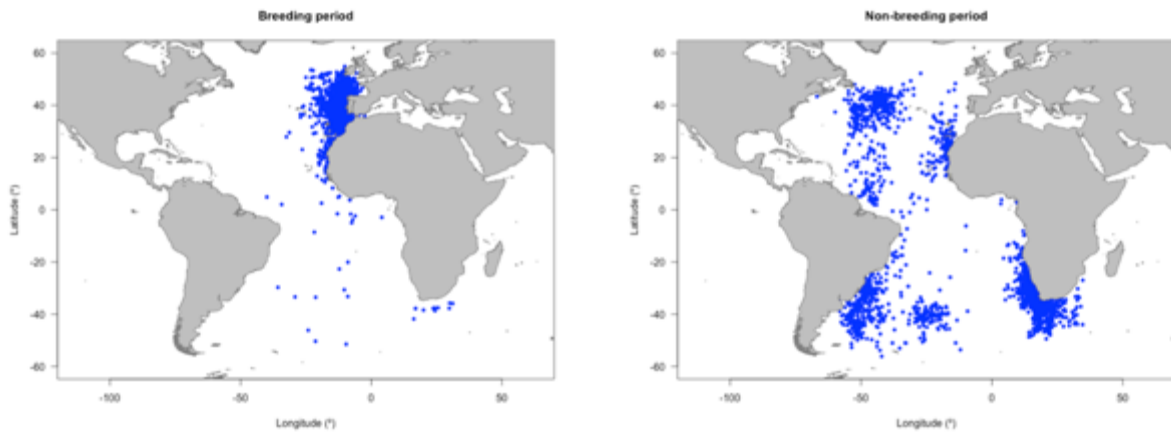
(B) Desertas petrel (N = 54, between 2007-2015)

(C) Macaronesian shearwater (N = 23, between 2011-2015)
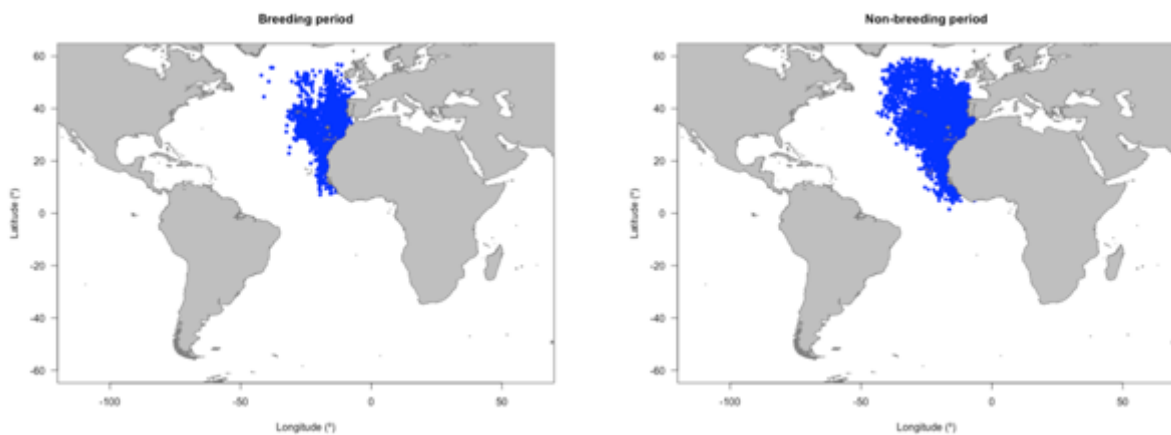
Figure 1. At-sea distribution of (A) Cory's shearwaters from Berlenga Island (mainland Portugal), (B) Desertas petrels from Bugio Island (Madeira) and (C) Macaronesian shearwaters from Cima Islet and Selvagem Grande (Madeira) during their breeding (left panels) and non-breeding (right panels) periods.

3.2 The influence of moonlight on seabirds' behaviour

During the breeding period, Desertas petrels and Macaronesian shearwaters spent a significantly higher time flying during full moonlight (Table 1 and Fig. 2A), foraged farthest from their breeding colony (Table 1 and Fig. 2B), at significantly higher depths (Table 1 and Fig. 2C) and under windier regimes (Table 1), when compared to Cory's shearwaters and all other moon phases. Plus, during full moon Macaronesian shearwaters visited significantly less times their breeding colony, when compared to Cory's shearwaters and Desertas petrels (Table 1 and Fig. 2D).

During the non-breeding phase and under full moonlight, Desertas petrels and Macaronesian shearwaters spent a significantly higher percentage of time flying (Table 2 and Fig. 3A), landed more often (Table 2) and foraged on windier habitats (Table 2 and Fig. 3B), when compared to Cory's shearwaters and all other moon phases. Still during full moonlight, more Cory's shearwaters and Desertas petrels departed on pre-breeding (Table 2 and Fig. 3C) and post-breeding (Table 2 and Fig. 3D) migrations, when compared to Macaronesian shearwaters and all other moon phases.

Table 1. Generalized Linear Mixed Models (GLMMs) testing the effect of the interaction between species (Cory's shearwater, Sch; Desertas petrel, Dpe; and Macaronesian shearwater, Msh) and moon phase (new, quarter and full moon) on foraging parameters and characteristics of habitats used by those seabird species during their breeding period. The individual was used as a random effect to avoid pseudo-replication issues. Significant results in bold. Effect was evaluated with post-hoc multiple comparisons with Bonferroni correction.

Foraging parameters	Cory's shearwater (Csh; N = 28)			Desertas petrel (Dpe; N = 54)			Macaronesian shearwater (Msh; N = 23)		
	New moon	Quarter	Full moon	New moon	Quarter	Full moon	New moon	Quarter	Full moon
% time spent flying	46.4 ± 4.6	53.0 ± 3.1	69.9 ± 5.6	68.9 ± 5.7	77.0 ± 3.2	89.9 ± 6.0	72.6 ± 4.0	81.4 ± 3.9	94.1 ± 6.3
% landings (per hour)	23.7 ± 1.7	27.1 ± 2.6	31.0 ± 1.8	30.2 ± 1.4	29.0 ± 1.3	32.7 ± 1.7	33.1 ± 1.6	35.7 ± 1.9	38.5 ± 1.6
% number of colony visits (per days tracked)	40.1 ± 3.8	36.1 ± 3.9	35.1 ± 4.4	42.1 ± 2.1	39.3 ± 2.0	26.9 ± 3.6	36.1 ± 2.2	33.4 ± 2.5	19.9 ± 1.9
Max. dist. to colony (m)	52.1 ± 8.2	59.2 ± 6.6	100.1 ± 30.2	192.0 ± 42.1	289.3 ± 62.4	908.0 ± 87.1	187.2 ± 42.1	201.1 ± 33.2	1682.2 ± 67.1
Characteristics of habitats used									
Depth (m)	35.0 ± 9.0	39.0 ± 9.0	55.0 ± 11.0	70.0 ± 9.0	102.0 ± 9.0	199.0 ± 12.0	82.0 ± 12.0	111.0 ± 17.0	289.0 ± 21.0
Sea surface temperature (°C)	17.4 ± 0.5	18.0 ± 0.3	19.7 ± 0.3	20.3 ± 0.9	21.1 ± 0.8	22.2 ± 0.5	19.8 ± 0.4	20.5 ± 0.5	22.1 ± 0.3
Chlorophyll a concentration (mgm-3)	1.6 ± 0.3	1.0 ± 0.4	0.9 ± 0.4	0.5 ± 0.1	0.7 ± 0.2	0.5 ± 0.1	0.8 ± 0.2	0.9 ± 0.3	0.4 ± 0.4
Wind speed (ms-1)	3.1 ± 0.5	2.9 ± 0.2	3.9 ± 0.4	3.6 ± 1.0	4.0 ± 0.2	6.1 ± 1.0	2.9 ± 1.1	3.8 ± 0.4	6.9 ± 1.2

| Foraging parameters	Species			Moon phase			Species * Moon phase		
	GLMM: $F_{(8,96)}$	P	Effect	GLMM: $F_{(8,96)}$	P	Effect	GLMM: $F_{(8,96)}$	P	Effect
% time spent flying	5.12	**< 0.001**	Dpe & Msh > Csh	2.89	**0.01**	Full moon > all others	2.55	**0.02**	Dpe & Msh; full moon > all others
% landings (per hour)	1.78	0.09	—	1.71	0.11	—	1.63	0.12	—
% number of colony visits (per days tracked)	3.71	**0.001**	Msh < all others	2.77	**0.01**	Full moon < all others	2.19	**0.04**	Msh; Full moon < all others
Max. dist. to colony (m)	2.79	**0.01**	Msh > all others	2.63	**0.02**	Full moon > all others	2.21	**0.04**	Dpe & Msh; Full moon > all others
Characteristics of habitats used									
Depth (m)	6.01	**< 0.001**	Csh < all others	1.81	0.09	—	2.59	**0.02**	Dpe & Msh; Full moon > all others
Sea surface temperature (°C)	2.86	**0.01**	Csh < all others	1.58	0.14	—	1.35	0.23	—
Chlorophyll a concentration (mgm-3)	2.25	**0.03**	Csh > all others	1.55	0.15	—	1.41	0.21	—
Wind speed (ms-1)	3.01	**0.01**	Dpe & Msh > Csh	2.45	**0.02**	Full moon > all others	2.29	**0.03**	Dpe & Msh; Full moon > all others
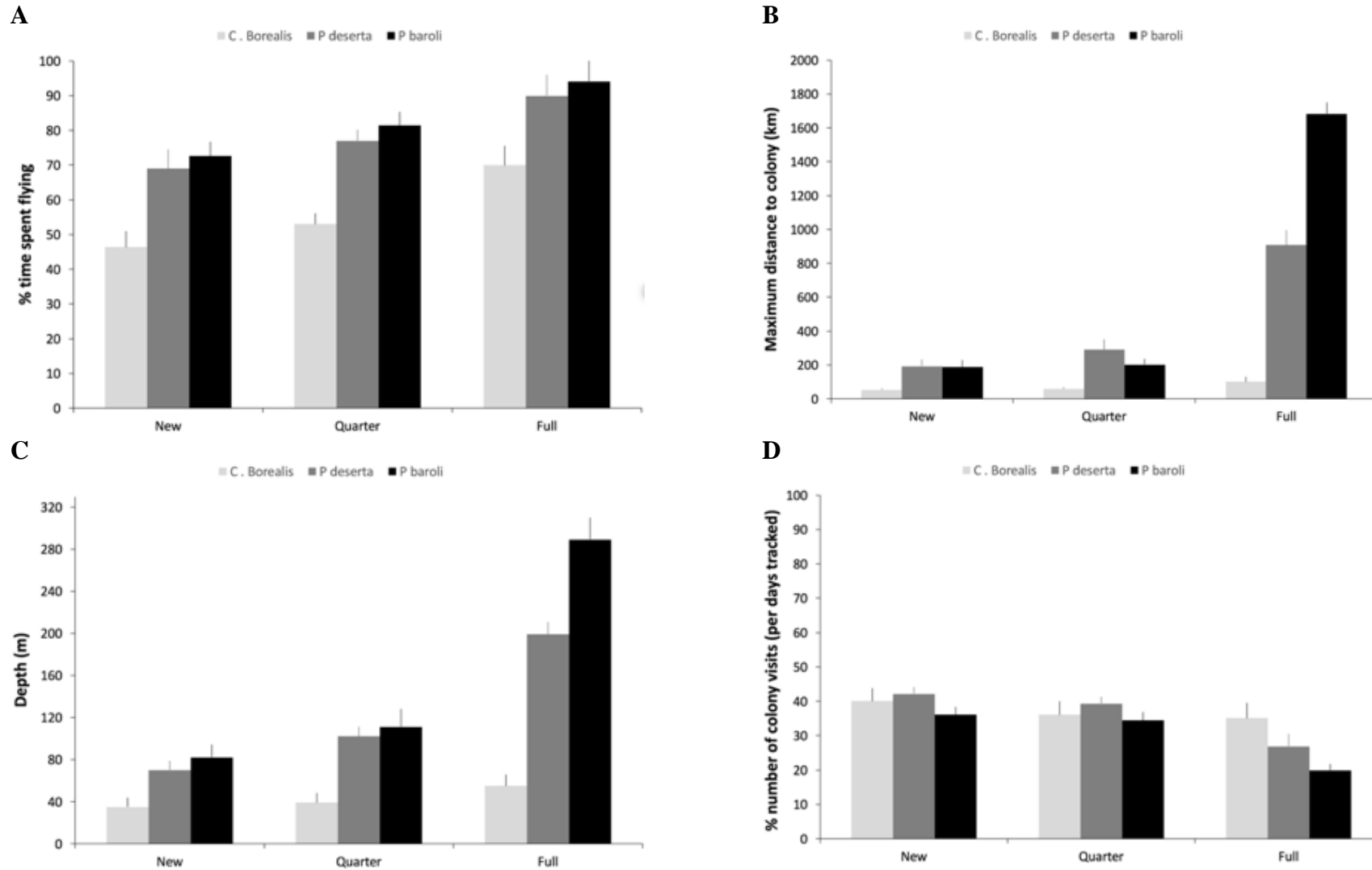
Figure 2. (A) Percentage of time flying during the night, (B) maximum distance to colony, (C) depth and (D) % number of colony visits of Cory's shearwaters (*C. borealis*), Desertas petrels (*P. deserta*) and Macaronesian shearwaters (*P. baroli*) during new (less than 30% of the moon illuminated), quarter (30–70%) and full (more than 70%) moon (http://aa.usno.navy.mil/faq/docs/moon_phases.php) of the breeding period of each seabird species.

Table 2. Generalized Linear Mixed Models (GLMMs) testing the effect of the interaction between species (Cory's shearwater, Sch; Desertas petrel, Dpe; and Macaronesian shearwater, Msh) and moon phase (new, quarter and full moon) on foraging parameters and characteristics of habitats used by those seabird species during their breeding period. The individual was used as a random effect to avoid pseudo-replication issues. Significant results in bold. Effect was evaluated with post-hoc multiple comparisons with Bonferroni correction.

Foraging parameters	Cory's shearwater (Csh; N = 28)			Desertas petrel (Dpe; N = 54)			Macaronesian shearwater (Msh; N = 23)		
	New moon	Quarter	Full moon	New moon	Quarter	Full moon	New moon	Quarter	Full moon
% time spent flying	22.1 ± 4.2	31 ± 2.1	57.9 ± 3.0	28.6 ± 2.3	38.2 ± 2.0	61.9 ± 1.9	39.9 ± 3.2	65.5 ± 5.5	78.3 ± 4.1
% landings (per hour)	24.0 ± 1.9	26.1 ± 2.1	29.9 ± 1.9	25.9 ± 1.8	31.4 ± 1.1	42.2 ± 1.9	28.0 ± 1.3	34.1 ± 1.9	49.3 ± 2.0
% departures for pre-breeding migration	13.6 ± 1.7	19.9 ± 1.5	66.5 ± 1.3	10.4 ± 1.1	20.8 ± 1.6	68.8 ± 1.5	23.9 ± 2.1	34.2 ± 1.7	41.9 ± 1.9
% departures for post-breeding migration	20.1 ± 1.0	25.3 ± 1.7	54.6 ± 1.1	19.6 ± 1.2	25.3 ± 1.4	55.1 ± 1.8	27.1 ± 2.0	34.5 ± 1.9	38.4 ± 1.7
Characteristics of habitats used									
Depth (m)	110.0 ± 19.0	110.0 ± 19.0	136.0 ± 23.0	98.0 ± 20.0	101.0 ± 32.0	141.0 ± 39.0	287.0 ± 23.0	317.0 ± 45.0	324.0 ± 35.0
Sea surface temperature (ºC)	16.3 ± 0.6	17.1 ± 0.4	18.9 ± 0.7	15.9 ± 0.5	16.7 ± 0.5	17.9 ± 0.3	20.7 ± 0.6	22.4 ± 0.6	23.0 ± 0.4
Chlorophyll a concentration (mgm-3)	2.1 ± 0.1	1.8 ± 0.5	0.9 ± 0.3	1.7 ± 0.3	1.0 ± 0.4	0.8 ± 0.3	0.8 ± 0.2	0.9 ± 0.3	0.4 ± 0.4
Wind speed (ms-1)	3.4 ± 0.7	3.6 ± 0.9	4.2 ± 0.8	4.7 ± 1.1	5.3 ± 0.9	7.6 ± 1.4	5.1 ± 1.0	5.5 ± 0.6	8.1 ± 1.3

Foraging parameters	Species GLMM: $F_{(8,96)}$	P	Effect	Moon phase GLMM: $F_{(8,96)}$	P	Effect	Species * Moon phase GLMM: $F_{(8,96)}$	P	Effect
% time spent flying	5.03	**< 0.001**	Msh > all others	2.77	**0.01**	Full moon > all others	2.69	**0.01**	Dpe & Msh; Full moon > all others
% landings (per hour)	3.69	**0.001**	Dpe & Msh > Csh	1.41	0.21	—	2.43	**0.02**	Dpe & Msh; Full moon > all others
% departures for pre-breeding migration	2.81	**0.01**	Csh & Dpe > Msh	2.49	**0.02**	Full moon > all others	2.13	**0.04**	Csh & Dpe; Full moon > all others
% departures for post-breeding migration	2.96	**0.01**	Csh & Dpe > Msh	2.39	**0.02**	Full moon > all others	2.05	**0.05**	Csh & Dpe; Full moon > all others
Characteristics of habitats used									
Depth (m)	3.03	**0.01**	Msh > all others	1.74	0.11	—	1.49	0.17	—
Sea surface temperature (ºC)	2.16	**0.04**	Msh > all others	1.56	0.16	—	1.43	0.21	—
Chlorophyll a concentration (mgm-3)	1.52	0.16	—	1.48	0.18	—	1.31	0.23	—
Wind speed (ms-1)	5.32	**< 0.001**	Dpe & Msh > Csh	2.88	**0.01**	Full moon > all others	2.52	**0.02**	Dpe & Msh; Full moon > all others
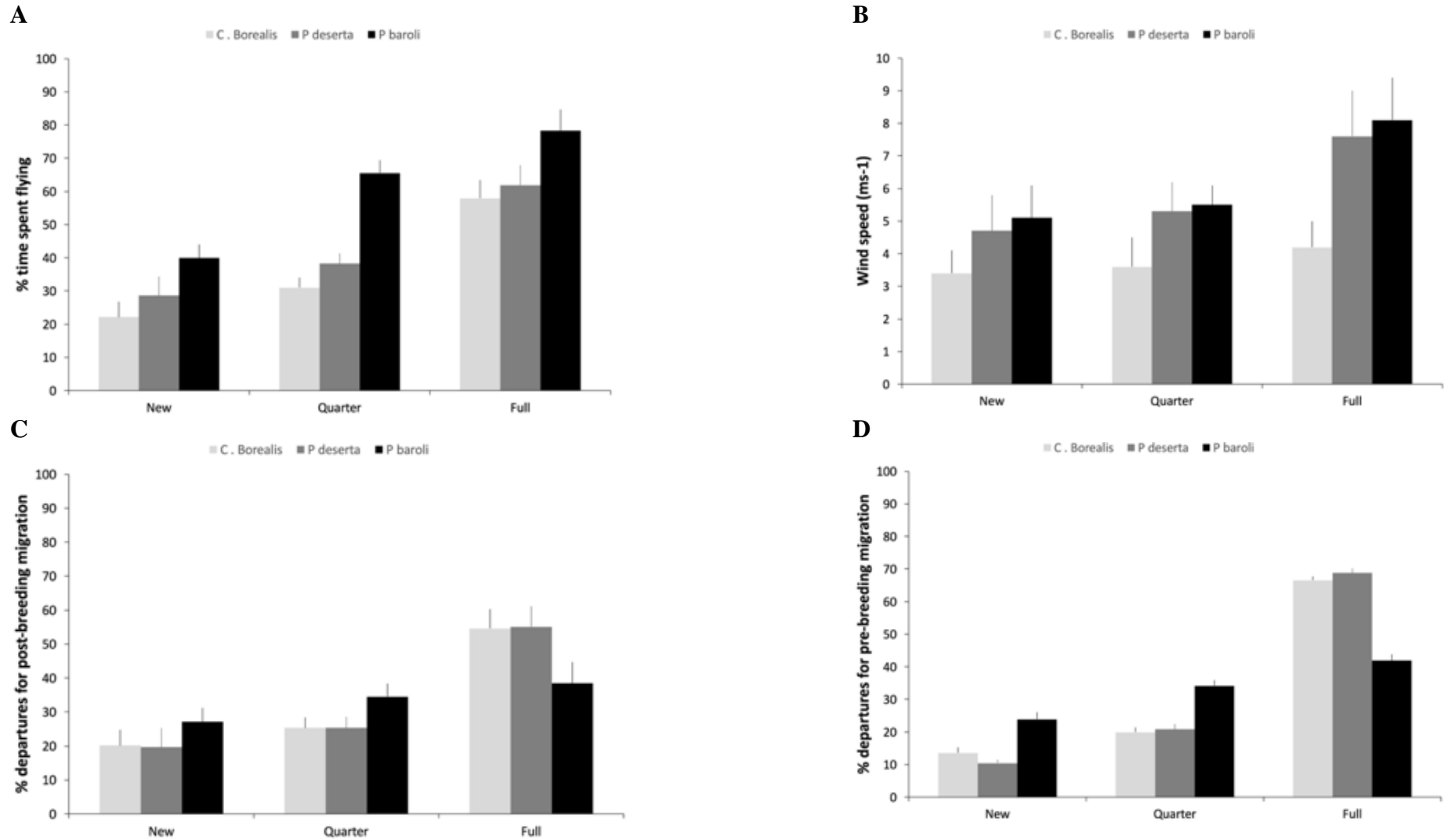
Figure 3. (A) Percentage of time flying during the night, (B) wind speed, (C) % of departures for the post-breeding migration and (D) % of departures for the pre-breeding migration of Cory's shearwaters (*C. borealis*), Desertas petrels (*P. deserta*) and Macaronesian shearwaters (*P. baroli*) during new (less than 30% of the moon illuminated), quarter (30–70%) and full (more than 70%) moon (http://aa.usno.navy.mil/faq/docs/moon_phases.php) of the non-breeding period of each seabird species.

Chapter IV – Discussion

Luís Ferreira

4.1 General discussion

4.1.1 At-sea activity

All three study species (Cory's shearwaters, Desertas petrels and Macaronesian shearwaters) showed a higher % of time spent flying during the full moon period. This has also been reported for other procellariforms like Barau's petrels (Pinet et al., 2011); White-chinned petrels (*Procellaria aequinoctialis*) (Mackley et al., 2011), Yelkouan Shearwaters (*Puffinus yelkouan*) (Bourgeois et al., 2008) Streaked Shearwaters (*Calonectris leucomelas*) (Yamamoto et al., 2008) Scopoli's Shearwaters (Rubolini et al., 2014), Fea's petrels (*Pterodroma feae*) or Zino's Petrels (*Pterodroma madeira*) (Ramos et al., 2016), which generally increased their activity at night with increasing moonlight. Thus, we can argue that the lunar cycle might be an important factor in the ecology of Procellariforms, two hypotheses can be set (1) is it an endogenous cycle or (2) is it because of a higher availability and/or visibility of prey under moonlight? The reason is not still fully understood, since few studies relate changes in the diet of nocturnal foraging seabirds with the lunar cycle (but see Waap et al., 2017).

The higher % of time spent flying during the breeding period might also be related with parents increasing their searching effort to provision their chick (Dias et al., 2012b; Ramírez et al., 2013; Paiva et al., 2016) plus the selectivity in prey choice, as parents are expected to select larger or higher-quality prey for their chicks (Wilson et al., 2004). Also is possible to observe that in full moon periods Deserta's petrels and Macaronesian shearwaters foraged farthest from their breeding colony, at significantly higher depths and under windier regimes (both during the breeding and non-breeding periods), demonstrating a higher effort, during moonlight condition, to catch prey from this two species compared to Cory's Shearwaters. This is possibly explained by Cory's shearwaters not being so dependent of preys performing diel migrations and being more available at the sea surface during full moon nights.

During the non-breeding period, as expected, this three species spent significantly less time flying and landed more often, this pattern could be directly linked to the fact that birds have a lower energetic demand during this period (Pinet et al., 2011), are less selective on their prey (Wilson et al., 2004), and can adopt a more 'sit and wait' technique, a behaviour also founded on Cook's petrels (*Pterodroma cookii*) (Rayner et al., 2008).

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4.1.2 Colony Attendance

Colony attendance was not similar between the three species, as expected, Macaronesian shearwaters and Desertas petrels were the most influenced by the lunar cycle and Cory's shearwaters much less or almost not influenced by the moon phase. The results have shown that during full moon, Macaronesian shearwaters and Desertas petrels not only have significant difference in the number of colony visits, but also that the number of visits decline almost half comparing to the new moon phase. Plus, when compared to Cory's shearwaters, these two species foraged much farther from their breeding colonies and because of these higher distances they probably were not able to visit the colony more often.

The decrease in colony attendance when moonlight is more intense seems to be a widely spread adaptation of many small-sized seabirds to avoid predation (Watanuki, 1986; Mougeot & Bretagnolle, 2000; Keitt et al., 2004; Riou & Hamer, 2008; Rubolini et al., 2014). Therefore, if these types of behaviours have in common the moonlight or the moon itself, and mostly can be explained by some sort of predation risk avoidance (Jones et al., 1989; Shealer & Kress 1991; del Hoyo et al., 1992; Mougeot & Bretagnolle 2000) the larger species was not so affected by this pressure of predation, showing a minor influence by the moon light (Mougeot & Bretagnolle 2000; Granadeiro et al., 2009;).

Nevertheless, and even though predation pressure seems to be the best plausible explanation for the observed pattern, we cannot exclude the possibility that during full-moon, the smaller Procellariiforms showed a higher activity at-sea, and therefore, if the species spend more time at-sea we naturally expected they will visit less the colony. Anyway, further research on colony attendance of this three species in colonies with and without predators is needed to disentangle the effect of predation pressure on this behavioural trait. In fact, we do not know whether avoiding colony attendance on brighter nights is an inherited specific trait, independent of predation pressure and/or other environmental factors, or if it is dependent on the conditions in each colony. Environmental factors are also known to influence prey availability and, consequently, foraging success and chick provisioning through diet composition, feeding frequency and amount of food per feeding event (Peck et al., 2004; Erwin & Congdon 2007; Devney et al., 2010). The diet of this three species is partly dependent on prey species performing diel vertical migrations (Paiva et al., 2010; Ramírez et al., 2013; Ramos et al., 2015), which are known to be negatively influenced by moonlight (Kinzer & Schulz, 1988; Catul et al. 2011;). Therefore, the lunar cycle can also influence colony attendance through prey availability at-sea.

By the results presented, we can assume, that the decrease on colony attendance patterns during full-moon periods, is possibly justified by the combination of these two important factors, (1) the predation risk at the colony plus (2) the environmental conditions at-sea, driving the species to spend more time at-sea and consequently visiting the colony less. Also, the predation pressure factor, can be confirmed, because in these three size different species the more suitable to predations, the smaller procellariforms (Macaronesian shearwaters and Desertas petrels) showed to be more influenced by the full-moon, but on the other hand, the larger wasn't influenced by this factor.

4.1.3 Migratory Movements

The three species showed a higher % of departures for pre- and post- breeding migrations during full moon periods. But still, during full moonlight, significantly more Cory's shearwaters and Desertas petrels departed on pre-breeding and post-breeding migrations, when compared to Macaronesian shearwaters and all other moon phases. It is worth mention that under full moon there was a higher % of individuals departing in pre-breeding migration than the % of individuals engaging in post-breeding migration. The higher synchronization of the first case should be related with the advantage of reaching the breeding grounds as early as possible, thus choosing/ competing for the best nesting borrows and starting earlier their breeding duties, with proved higher breeding success (Warham, 1990; Alerstam, 2006).

Previous studies about migration of these species showed that some individuals of Cory's shearwaters and Desertas petrels perform trans-equatorial migrations (Dias et al., 2012a; Ramírez et al., 2013), while Macaronesian shearwaters remain in the North-Atlantic region (Ramos et al., 2015; Paiva et al., 2016;). Since trans-equatorial migrations are long-distance movements, it is normal that these individuals try to minimize the time of the migratory journey, thus expending the lower risk and energy possible on this type of migration. It is possible that some birds could use moonlight to detect visual cues and orient themselves in their migratory path, like they take advantages of higher illumination to pursue prey (Phalan et al., 2007), and adopt a 'fly and forage strategy' during these trips (Strandberg & Alerstam, 2007), making stopovers in productive areas to refill their energy budgets, before re-engaging in migration (Ramírez et al. 2013). Thus, for these long-distance migrants, synchronization should be crucial, so they depart around the environment factors which allow the faster migration, in this case around full moon.

If there is a link between migratory distance and synchronization with the moon phase, the shorter the migration route until the non-breeding destination, the less the migrator would be influenced by the occurrence of full moon. In our study, Macaronesian shearwaters, were less influenced by this factor, thus kind of confirming the former assumption that long-distance migrators opt to wait for better conditions to migrate. It is already known that some procellariforms have a certain degree of consistency on the dates of departure and arrival dates to the colony (Dias et al., 2011; Pinet et al., 2011; Ramírez et al., 2016), but in many of those studies the authors did not address the possible moon effect on the timing of those movements. Therefore, more studies linking the size of migration and departure date in relation to the moon stage should be conducted.

4.2 Conclusion

Overall, our results show that under full moonlight, besides the endogenous and/or specific species traits hypothesis, small sized procellariiforms (Macaronesian shearwaters and Desertas petrels) increased their at sea activity (e.g. more time spent flying), in order to take advantage of the higher visibility therefore increasing the "foraging effort" and consequently increase their foraging success. Is also important to refer they foraged in more pelagic, high depth and windier domains, showing some kind of selectivity during this full moon periods. They also, decreased their colony attendance when compared to a larger sized procellariform (Cory's shearwater).

Full moon also dictated a higher number of departures in pre- and post-breeding migrations for the trans-equatorial migrants (Cory's shearwaters and Desertas petrels) but not for the resident species (Macaronesian shearwater).

Nevertheless, further studies in this and other procellariiforms, are necessary to fully understand the relation between the moon cycle and the patterns observed. Whether they are due to a behavioral adaptation characteristic of the size of the species or/and if it is simply a result of exogenous environmental conditions is yet to be understood.

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Annex 1. At-sea distribution of Cory's shearwater during pre-breeding migration (March), breeding (April – September), post-breeding migration (October) and non-breeding (December-February) phases (Missagia et al. 2015 Mar. Biol.).
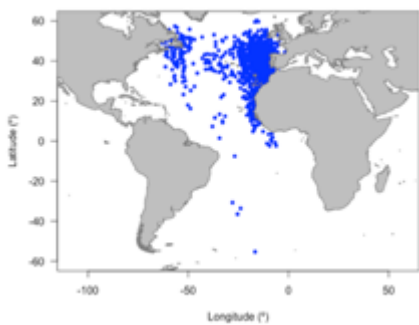
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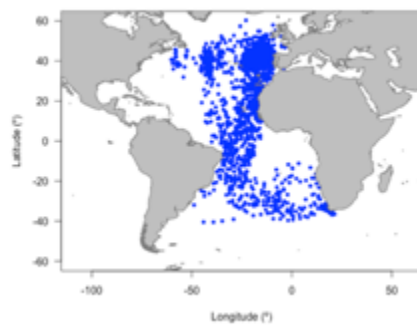
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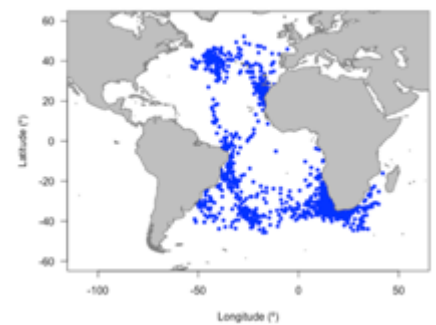
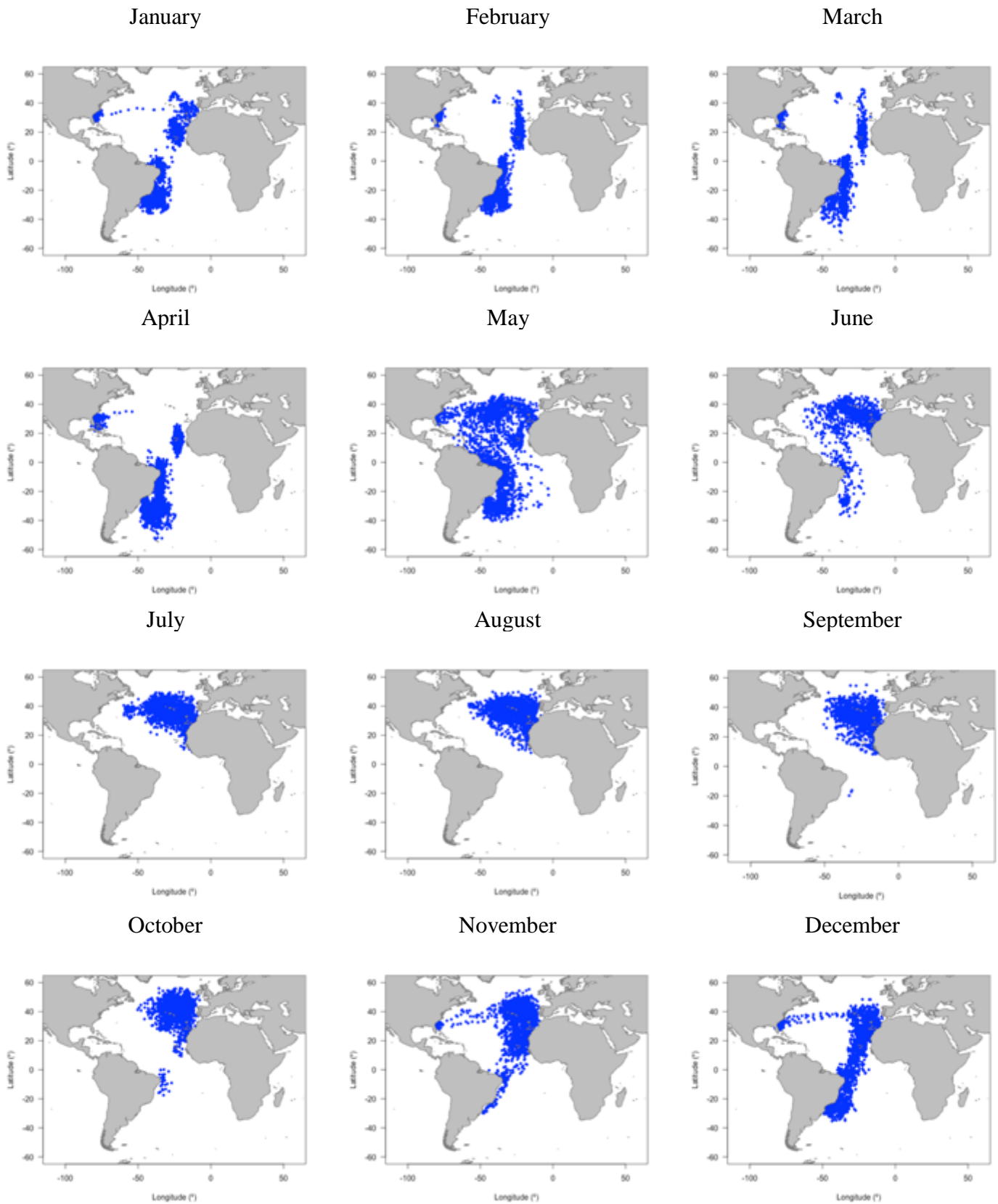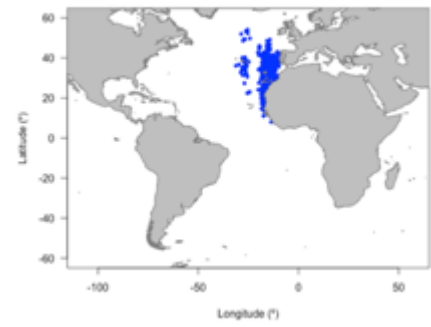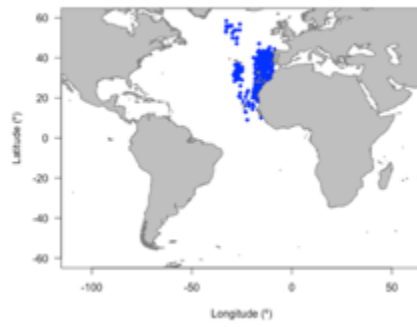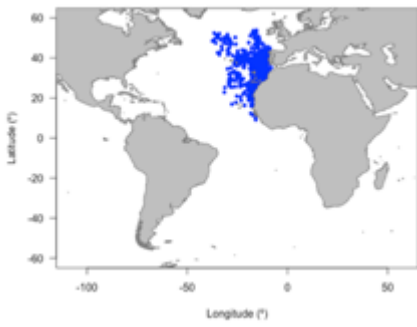March

April

May
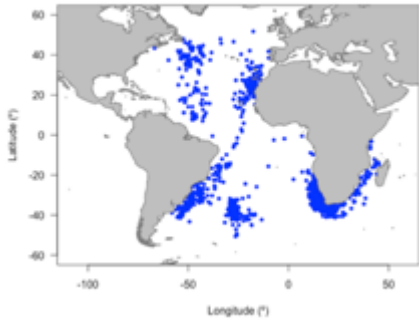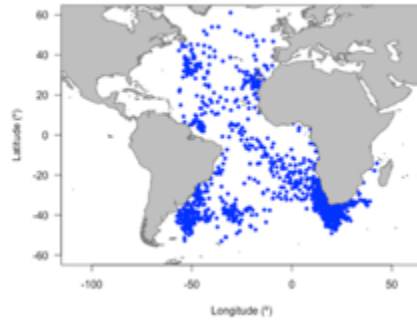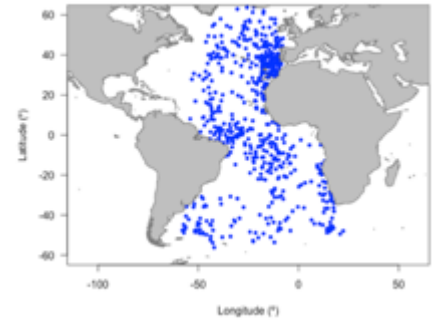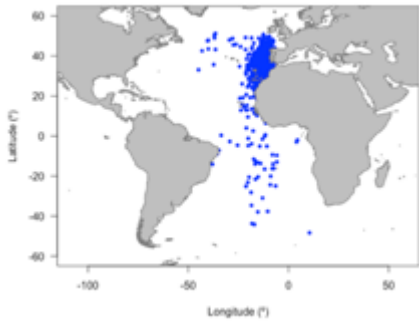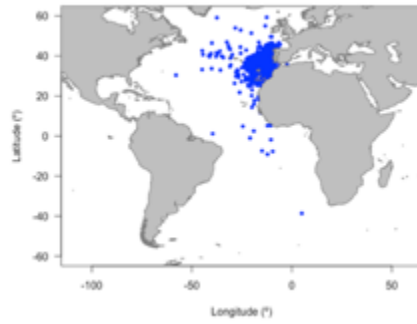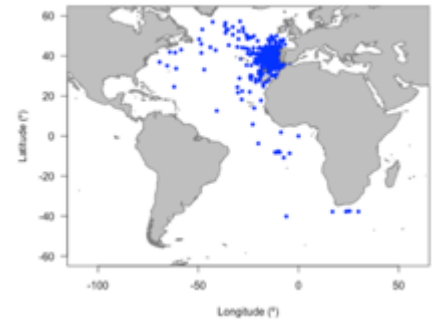
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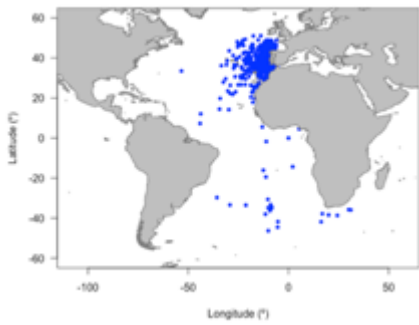
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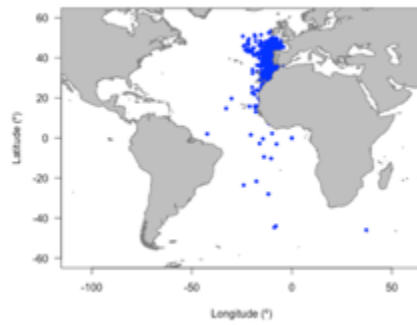
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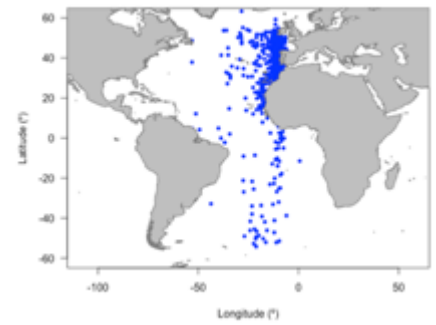
October

November

December

Annex 2. At-sea distribution of Desertas petrel during pre-breeding migration (May), breeding (June – November), post-breeding migration (December) and non-breeding (January – April) phases (Ramírez et al. 2013 MEPS).

Annex 3. At-sea distribution of Macaronesian shearwater during pre-breeding migration (November), breeding (December – May), post-breeding migration (June) and non-breeding (July – October) phases (Paiva et al. 2016 PlosOne).
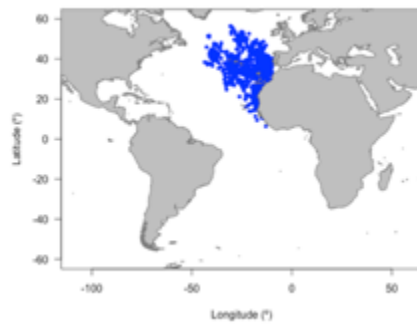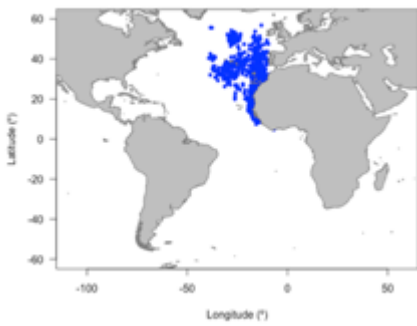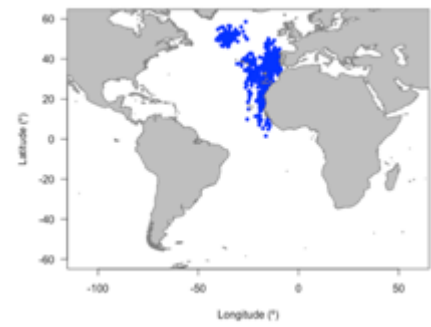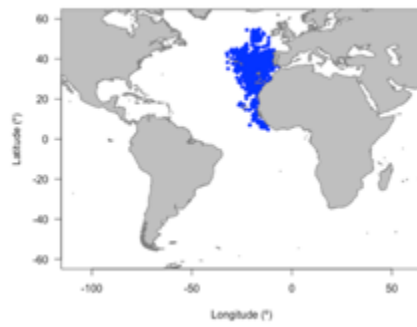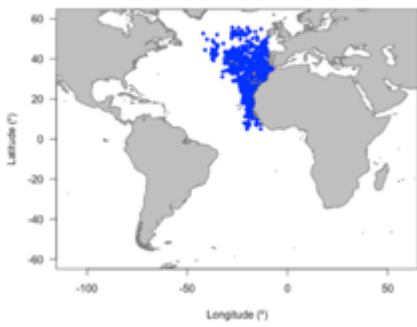

January

February

March

April

May

June

July

August

September

October

November

December