DEPARTAMENTO DE CIÊNCIAS DA VIDA

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UNIVERSIDADE DE COIMBRA

# Environmental driven sexual segregation in a marine predator

Justin da Silva Pereira

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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 Professor Doutor Jaime Albino Ramos (Universidade de Coimbra) e do Doutor Vítor Hugo Rodrigues Paiva (Universidade de Coimbra).

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## Abstract

A knowledge of pelagic seabird foraging patterns is important to evaluate key areas for marine pelagic top predators. The main objective of this thesis was to describe the sex-driven foraging patterns of a pelagic top predator - Cory's Shearwater, *Calonectris borealis* - breeding in the small island of Berlengas, Portugal, during the chick-rearing seasons of 2010-2014. We identified the environmental predictors that determine the selection of foraging areas by female and male Cory's Shearwaters and the role of breeding experience in this process. This medium-term study also assessed, in a scenario of climate stochasticity, the ecological impacts of climatic conditions in marine environments and the possible change in the distribution of this species in the North Atlantic, considering the increase in sea surface temperature and given the vulnerability of seabird predators to extreme climatic events. We studied the foraging distribution of fifty-five male and female Cory's shearwaters with GPS tracking devices during the chick-rearing period between 2010 – 2014, and accessed their trophic choices with stable isotope analysis (SIA) of their plasma. The study sample was also divided between experienced and inexperienced individuals using the total number of breeding attempts as a proxy for experience, and the prediction that reproductive success typically increases with breeding age and experience in seabirds. This study benefited from a long-term database of the breeding population, such that minimum age, sex and previous breeding experience were known for most of the individuals. We found spatial segregation of female *versus* male Cory's Shearwaters as well as inexperienced *versus* experienced breeders, which increased during the last couple of years. Males relied heavily on static variables like the bathymetry of the area, while females were much more explorative, having a different combination and weighting of important variables (i.e. productivity proxies). Females undertook much larger foraging journeys than males, in years of greater environmental stochasticity. Finally, climate stochasticity might have a significant influence on the spatial distribution of the species, exercising greater influence on male and experienced individuals (i.e. the group showing a more static distribution). Nevertheless, the true effects of such large-scale events cannot be encompassed on such a short-term study, making the continuity of monitoring the foraging ecology of this species crucial to understand the impact of climate change on this and other marine taxa.

**Keywords**: Sex-driven foraging segregation, Breeding experience, *Calonectris borealis*.

## Resumo

Um conhecimento dos padrões da ecologia de aves marinhas, representa uma contribuição importante para compreender quais as áreas de alimentação destas aves e o porquê de estas as escolherem. Permite ainda conhecer, de que modo é que a presença de condições ambientais adversas influencia o comportamento destas aves. O principal objetivo desta tese foi descrever os padrões comportamentais de ambos os sexos de um predador pelágico, tendo como modelo de estudo a Cagarra, *Calonectris borealis*, reprodutores na pequena ilha da Berlenga, Portugal, durante o período de desenvolvimento das crias de 2010 a 2014. Foram identificados os principais fatores ambientais que influenciam a seleção e os seus padrões de alimentação, e qual o papel do sexo e da experiência de indivíduos nestas escolhas. Este estudo de médio-prazo também reflete, num cenário de mudanças climáticas, os impactos ecológicos que estes terão em ambientes marinhos e a qual a possível alteração na distribuição desta espécie no Atlântico Norte, considerando o aumento da temperatura da superfície do mar e a vulnerabilidade destes predadores face a eventos climáticos extremos. Para dar resposta a estes objetivos, utilizamos dispositivos GPS para acompanhar indivíduos desta população durante os quatro anos deste estudo e comparamos os resultados com a sua ecologia trópica através de análises isotópicas. Em seguida, analisamos as diferenças na distribuição espacial e comportamental de cinquenta e cinco indivíduos pertencentes a esta população de Cagarras reprodutoras na costa litoral portuguesa. O grupo foi dividido entre indivíduos experientes e inexperientes usando o número total de tentativas de acasalamento como um indicador para a experiência, e a suposição de que o sucesso reprodutivo normalmente aumenta com a idade e a experiência em aves marinhas. Este estudo beneficiou de um conhecimento de longo prazo da população alvo, sabendo *a priori* dados como a idade mínima das aves, o sexo e o historial do sucesso reprodutor para a maioria dos indivíduos. Através da análise de isótopos de azoto e carbono do plasma e sangue destas aves, inferimos qual o efeito da experiência de um individuo na seleção de presas na sua ecologia trófica. Os resultados confirmam a existência de segregações espaciais entre machos e fêmeas, assim como de aves experientes e inexperiente. As principais variáveis ambientais que influenciaram a distribuição espacial de indivíduos do sexo feminino foram a distância à colónia e a temperatura da superfície do mar, fazendo com que adotem um comportamento mais exploratório e pelágico em anos de maior estocacidade. Por sua vez, nos indivíduos do sexo masculino essas variáveis dizem respeito à profundidade da água e das concentrações de clorofila a. Os resultados deste estudo mostram ainda que o aquecimento global pode exercer influência significativa sobre a distribuição espacial da Cagarra, especialmente em aves experientes (que apresentam uma distribuição mais estática). No entanto, os verdadeiros efeitos de tais eventos de grande escala não podem ser englobados num estudo de tão pequena duração, tornando a continuidade de monitorização ecológica desta espécie cruciais para entender o impacto das mudanças climáticas sobre este grupo de animais marinhos.

**Palavras-chave**: Segregação espacial, Experiência reprodutiva, *Calonectris borealis*

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# Chapter I - Introduction

## 1.1 Marine environment and Marine top predators

Marine environment ecosystems are complex adaptive systems, among the most diverse on Earth, linked across multiple scales by flow of water and species movements (Levin and Lubchenco 2008). The immense oceans encompass habitats ranging from highly productive coastal regions to much less productive deep-sea environments. Taking into account the size of such ecosystems, their resources are sparse and scattered over large areas, making their location largely unpredictable (Weimerskirch et al. 2007). Oceans are subdivided into several ecosystems based on different characteristics of depth, oceanography, productivity and populations of organisms that are linked in trophic food chains and webs (Sherman 1993). They also experience seasonal patterns in primary productivity, particularly at higher latitudes, leading to changes in predator distributions. As marine productivity tends to be distributed heterogeneously, with high productive areas located close to specific locations such as shelf edges or coastal upwellings (Ainley and Boekelheide 1990; Bakun 1990; Crawford 2007), marine organisms such as fish are found in patches of different sizes, depending on the process concentrating them and on the specific behaviour of the species. Oceanographic phenomena such as ocean currents, winds or river influx introduce varying complexities in the interlinkages between biotic components and environmental characteristics especially in the coastal waters (Chen et al. 2004; Tweddle et al. 2010; Wetz and Wheeler 2004). Wind-driven coastal upwellings consists on the rise of cold and deep subsurface waters that are rich in nutrients, and contribute for an increase in the density of primary producers such as phytoplankton, which will consequentially attract zooplankton, followed by zoo – and phyto – planktivorous pelagic fish which in turn will attract top predators such as large fish, cetaceans or seabirds (Malik et al. 2015). Such diversity in vertebrate and invertebrate communities allow top marine predators such as seabirds to specialize, coping with this unpredictable location of prey by adopting specific foraging strategies perfected by strong natural selection processes (Hunt & Schneider 1987; Weimerskirch 2007). Within such diverse and dynamic environments, animals seek highly productive areas, by changing their foraging grounds and strategies, determined by species dispersal capacity and energy requirements, which may vary during the annual cycle (Green et al. 2009). Altering foraging grounds also depends on food availability in order to fulfil their energetic requirements and, consequently, maximizing fitness (Polovina et al. 2001; Péron et al. 2010).

Top marine predators are important top consumers in marine environments, having major influence in ecological processes that occur in these ecosystems (Scheriber and Burger 2001; Werner 2010; Paiva et al. 2013a). Such predator, including marine mammals, large teleosts, seabirds and sharks, occupy high trophic levels in marine habitats, and have been declining worldwide (e.g. Estes et al. 2006; Myers and Worm 2003; Baum et al. 2003; Pauly et al. 1998). Many studies show that the decline of these populations can have cascading effects on lower trophic levels on both coastal and pelagic areas (Myers and Worm 2003; Scheffer et al. 2005; Heithaus et al. 2008). In fact, declines in top predator abundance often alleviate predation pressure on meso-consumers, which indirectly increase the mortality rate of resource species (Myers et al. 2007; Scheffer et al. 2005). The loss of top predators is thus predicted to cause numerical increases in meso-consumers and declines in resource species. Due to the position and importance that top predators undertake in the food chain, they usually are considered indicators of the status and performance of the marine ecosystems. These conditions also qualify them as good subjects for ecological studies and favour the development of research programs aimed at identifying and analysing any trends that could lead to the better understanding and management of marine ecosystems, potentially preventing deregulation of ecological processes and disruption of ecosystem services (Block et al. 2011). Given the conspicuity of seabirds as marine predators, they play an important role as sentinel organisms because unexpected changes in their numbers, health or breeding success provide an alarm that may indicate an unknown pollution or food supply problem (Furness and Camphuysen 1997).

## 1.2 Procellariiformes seabirds

The tubenosed seabirds (albatrosses, petrels and shearwaters) are well known for their pelagic wide-ranging lifestyle. These long-living cosmopolitan birds spend most of their life at sea and are tied to small oceanic islands only for breeding (Dell'ariccia et al. 2010). The Procellariiformes order includes four families: Hydrobatidae (storm petrels), Pelecanoididae (diving petrels), Diomedeidae (albatrosses), and Procellariidae (shearwaters), and has the most long-lived species among birds (Bried 2003; Werner 2010). Generally, most species belonging to this group are colonial and gather annually in large numbers at somewhat few locations in order to reproduce (Piatt and Sydeman 2007). They present extreme life history strategies, such as the laying of a single egg per breeding season, followed by a long incubation and chick rearing period (Warham 1990; Schreiber & Burger 2001).

The evolution of aggregated breeding systems, generally referred to as colonies, is believed to have benefited from information exchange, cooperation, efficient defence against predators and several other benefits (Wittenberger and Hunt *1985*; Danchin and Wagner *1997*; Brown and Brown *2001*). Breeding is generally considered one of the most energy-consuming phase because of the high resource expenditure that it involves (egg production, nest attendance etc) and the constraints that it generates. Pelagic birds are true sea travellers during most of the year, but during the breeding season are central place foragers that need to return to the colony regularly, to incubate their eggs or attend their chicks. During this period, they are forced to commute between their colonies and pelagic feeding zones at sea to provision their offspring (i.e. central-place foraging behaviour; Jouventin & Weimerskirch 1990). This strategy imposes energetic constraints which limit foraging range and thus accessibility of certain marine habitats. Breeding occurs generally during summer, when productivity is highest. During the non-breeding season, birds can disperse over wide areas or migrate to completely different habitats as they no longer need to be central-place foragers (Shaffer et al. 2006; Bost et al. 2009a; Egevang et al. 2010).

Despite the advantages of breeding in large aggregations, there are distinct costs such as competition for resources or disease transmission, and the complex trade-off between costs and benefits leads to large variation in colony size across species, space and time (Wittenberger and Hunt *1985*; Brown and Brown 2001). Although a great understanding of these animal’s life style and their functional ecology in environments with high unpredictability of food resources, has been achieved in the last decades, most of the information regarding the group is based on the reproductive phase of their life cycles. Such knowledge has been gathered especially during the chick-rearing period, when food and energy demand is augmented, and when the birds have their distribution restricted to the surroundings of their breeding colonies, making them easier to handle and track (Paiva et al. 2010a; Haug 2015). Throughout the non-breeding season, seabirds are not bound to return to their nests, and usually take on migratory routes that can cover many thousands of kilometres into remote oceanic areas. Due to the inherent difficulty in equipping and tracking seabirds for a long period of time, and through such distances, information about the non-breeding period is still relatively scarce (i.e. when compared to the breeding season; Wilson et al. 2002).

### 1.3 Environmental variability

It is known that seabirds forage over conspicuous regions, where ocean productivity is naturally enhanced due to several oceanographic features and processes, which include upwelling areas associated with continental shelves (Louzao et al. 2006) or seamounts (Morato et al. 2008b); water mass properties like temperature (Paiva et al. 2010b) or salinity (Ainley et al. 2005); processes like tidal currents (Becker et al. 1983; Hunt et al. 1998); fronts (Spear et al. 2001; Bost et al. 2009) and thermoclines (Navarro & González-Solís 2009); distance to shore (Briggs et al. 1987) or colony (Hunt Jr. 1997); and wind conditions (Garthe et al. 2009). Tremblay et al. (2009) concluded that the relative importance of diverse environmental predictors of marine productivity depend on several factors, such as the species considered, sex, breeding status, locality and scale of the study. It is most likely that Procellariiformes take advantage of their dimethyl sulphide (DMS) olfactory capabilities in searching for advantageous areas (Nevitt 1999; Nevitt et al. 2002), and then might use visual cues to locate prey at smaller scales (Tremblay et al. 2009).

These processes have been affected greatly by climate change, which is closely related to large-scale atmospheric phenomena, correlating changes observed in atmospheric circulation with changes in oceanic circulation. This typically leads to harsh outcomes in biological processes throughout food webs all across the oceans. One of the best known large-scale atmospheric phenomena associated with climate change is the North Atlantic Oscillation (NAO) (reviewed by Stenseth et al. 2003). The NAO refers to a north−south alternation in atmospheric mass between the subtropical Atlantic and the Arctic and therefore involves desynchronised behaviours between the climatological low-pressure centre near Iceland and the high-pressure centre near the Azores (Hurrell et al. 2003). The effects of NAO over the north Atlantic varies regionally (Stenseth et al. 2003). For instance, along the Portuguese Current system a negative NAO index indicate a perceptible decrease in the sea surface temperature (SST), caused by strong winds that toughen the upwelling phenomenon. This in turn can be related to an overall increase in abundance and accessibility of marine organisms from lower trophic levels, to top marine predators (Mann & Lazier 2006).

Paiva et al. (2013a) concluded that dramatic changes in the distribution and foraging behaviour of Cory’s shearwaters during 2010, comparatively to previous years seems to have been mostly related to a climatic event that occurred during the winter of 2009-2010. This climatic phenomenon was clearly depicted by a record-breaking negative NAO index (Osborn 2011), which significantly affected the productivity and decreased the abundance of pelagic prey fish, which in turn altered the foraging and feeding ecology of Cory's shearwaters and decreased their reproductive success. These negative trends in the abundance of pelagic prey cause great concern because not only does the NAO affect these lower trophic organisms but they also suffer the influence of intensive commercial fishing activities. (Paiva et al. 2013a). Overall, It seems that for the Portuguese Current system, moderate either negative or positive values of the extended winter NAO index are indicative of higher prey availability months latter (i.e. spring-summer), when Cory's shearwaters are breeding. While more severe (i.e. far from zero), either negative or positive, extended winter NAO index values leading to a notorious decrease in prey availability, and thus an altered foraging pattern and low reproductive success for Cory's shearwaters (Paiva et al. 2013a; Haugh et al. 2015).

## 1.4 Trophic markers

Understand and reporting how animals exploit their environment and how they cope with seasonal variation in resource abundance has been a major question in ecology (Johnson 1980; Wilcove & Wikelski 2008). Migratory animals depend on multiple regions (e.g.,non-breeding, breeding and migratory stop-over sites) and therefore these species may be more vulnerable to environmental perturbations than sedentary species (Wilcove & Wikelski 2008; Forman & Godron 1986; Kelly et al. 2005). For example, anthropogenic alteration within a species' breeding range may cause decreased breeding success (Robinson & Wilcove 1994) and disturbance at stop-over sites may affect the ability to refill fat reserves (Blem 1980; Moore et al. 1995). Hence, conservation management of animal populations depends on an understanding of these trophic and spatial ecology behaviours (Aarts et al. 2008).

As previously stated, marine ecosystems are highly heterogeneous environments in which productivity is controlled by physical features and processes, and the spatial ecology of seabirds at sea will have a direct influence on the prey that these animals exploit and consequently on their diet composition (Haury et al. 1978). The study of seabird foraging behaviour has always been hampered by the problem of assessing at-sea distribution, individuals being particularly difficult to track (Votier et al. 2010). Stable isotopic analysis (SIA) of biological tissues are often used to measure the isotopic signatures of seabirds and thus interpret their trophic choices. The rationale of using SIA is generally based on the assumption that when stable isotope signatures are incorporated in the proteins of consumers, they reflect those of the proteins in their diet in a predictable manner (Post 2002; Bearhop et al. 2004).

Stable isotope signatures can then be a fundamental alternative to the conventional ways of analysing diets, i.e. through collecting stomach contents or faeces (Cherel et al. 2007), and may simplify the monitoring of changes in marine ecosystems. Stable isotope ratios of Carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and Nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) are most commonly used in seabird stable isotope ecology (Ramos and González-Solís 2012). The use of $\delta^{15}N$ is based on the trophic richness of $^{15}N$ as we go up on the trophic web (Forero and Hobson 2003). According to Bond and Jones (2009), in each trophic level the $^{15}N$ values increase 3 to 5% due to the production of urea, since the $^{14}N$ is preferentially excreted in comparison with $^{15}N$. On the other hand, the use of

$\delta^{13}C$ on the marine environment is based on the $^{13}C$ gradient, because $^{13}C$ enriches from offshore to inshore regions, from benthic to pelagic strata of the water column and with decreasing latitude, allowing $\delta^{13}C$ to behave like a geographical indicator of foraging habitats (Cherel, Hobson & Weimerskirch 2000; Forero and Hobson 2003, Quillfeldt, McGill & Furness 2005; Cherel et al. 2006).

Depending on tissue-specific isotopic turnover, stable isotope measurements reflect average dietary records over days (blood plasma) to years (feathers) and have thus the potential to portrait nutritional variation at different time-scales (Dalerum & Angerbjörn 2005) as isotopic forms are fractioned and incorporated in new formed tissue through diet at specific temporal or spatial scales (Cherel et al. 2007). For instance, feathers allow us to analyse a period of information correspondent to the time of feather growth but, in contrast, red blood cells represents a period of a few weeks and plasma to about 7 days (Cherel et al. 2005; Hobson 2005). To infer geographical positions with isotopic analyses, the most reliable materials are those that are metabolically inactive so they retain signatures during a fixed growth period (Hobson 2005). As reported by Forero and Hobson (2003), keratinous materials such as feathers are particularly suitable because keratin is metabolically inactive and conserves dietary signals integrated over the period in which they grew. Moult patterns of bird feathers are seasonally predictable and consistent over time (Inger and Bearhop 2008; Ramos et al. 2009).

The great benefit of using such techniques over stomach regurgitations for instance, is that it provides not only information about the food ingested in the sort-term (like a snapshot picture of the individual diet) but also the food that was assimilated by tissues (from short- to long-term depending on the tissue). Conventional dietary analysis are also more prone to misinterpretations of the proportions of some food sources, due to the diverse rates of digestion of different prey types. Lastly the gathering of feather and/or blood samples is less stressful for the bird than the collection of diet samples by flushing their stomach contents (Paiva et al. 2010a).

## 1.5 Tracking devices

Seabirds spend most of their time at sea and are challenging to observe when not attending nests during the breeding season. Although they are considered the most threatened group of birds worldwide, conservation efforts were traditionally centred on threats faced at their breeding grounds (Ramirez et al. 2008) which are beneficial but highly insufficient, lacking the insight of the quality, location and extent of their feeding grounds which have crucial importance for the breeding success and survival of these marine top predators (Davis et al. 2005). Research has been therefore biased toward land-based observations, with the at-sea biology of smaller species generally limited to counts of travelling and foraging birds from opportunistic or research vessels which has also provided insight into the distribution and at-sea behaviour of these animals. Such studies are time or area restricted and unable to give detailed insights, such as distinguishing breeding status, sex or even species (Grecian et al. 2012), limiting the data and insights of the foraging behaviour of such individuals (Weimerskirch et al. 2005a). Also, the presence of vessels alters the normal behaviour of the birds and are normally associated with high costs (Grecian et al. 2012).

However, knowledge of foraging behaviour is essential to understand both the ecological roles of seabirds and constraints acting upon them in marine ecosystems (Wilson et al. 2002). The most productive and cost-effective way to study the flight and foraging behaviour of birds at sea employs electronic devices attached to individuals (Wilson et al. 2002; Daunt et al. 2003; Garthe et al. 2007). A variety of loggers and techniques have been revolutionizing the study of habitat foraging and selection, being developed and improved during the last 40 years (Grémillet et al. 2000; Hamer et al. 2007; Weimerskirch and Wilson 2000), equipped with increasing availability of remotely sensed data, computation power and the sophistication of analytical methods (Fauchald & Tverraa 2003; Ballance et al. 2006, Tremblay et al. 2009).

Since 1990 there was an upgrade of the technology used to study seabird ecology at sea, with the use of satellite telemetry (platform terminal transmitters [PTTs]), accurate devices (1-3 km) with solar power improved lifespan that do not require recovery for data processing. (Weimerskirch and Jouventin 1990). Presently two types of devices are heavily used to study seabirds: Global location sensing or geolocation (GLS) and global positioning system (GPS). Geolocation uses changes in ambient light levels to estimate sunrise, sunset, day length, and hence, longitude and latitude. The spatial resolution of these devices can be improved with the addition of temperature sensors to record long range movements (Burger & Shaffer 2008). One of the most recent tracking devices to come on line are GPS devices. These are unlimited in range and are capable of much higher resolution and accuracy than satellite transmitters or conventional radio telemetry (Hulbert and French 2001; Hünerbein et al. 2000). As with most new technologies, the first GPS data loggers were too heavy to deploy on all but very large-bodied seabirds such as albatrosses (Diomedae; (Waugh et al. 2005; Weimerskirch et al. 2002) and gannets (Sulidae; (Grémillet et al. 2004). The possibility of recording locations every second at accuracies within meters of true location and, the rather inexpensive price and small size of such devices have made them suitable enough to be used in several seabird species. The latest equipment, with package sizes in the range of 8-12 g, bring small and medium-sized seabirds (c. 300 g and larger) into the scope of possible applications. Currently, attachment of miniaturized sensors linked to data loggers has been popularized since these loggers do not call for long-distance signal reception and are lightweight devices with unmatched precision useful for identifying key habitat areas. However, as with GPS or GLS recorders, the limitation is that birds have to be recaptured or pass close to a remote data-recovery system to download the information, and thus involves a risk of losing data (Wilson et al. 2007, Burger & Shaffer 2008). The only time where birds faithfully return to the colony is during the breeding season, so most of the information available is restricted to this period of their life cycle. Tracking studies should control for adverse effects of the transmitter load and biases, and although it has been questioned (Barron et al. 2010, Kidawa et al. 2011) Burger and Shaffer (2008) propose a guideline, recognizing that behavioural and fitness changes can be avoided by keeping the transmitter weight below 3% of the bird’s body weight (Phillips et al. 2003). The studies performed by using this type of technology has already contributed significantly to conservation planning and monitoring of several species according to BirdLife International (www.birdlife.org/).

## 1.6 Foraging strategies in relation to age and breeding experience

Marine predator foraging behaviour depends largely on the distribution, abundance and reliability of their prey (Staniland et al. 2006), but also on intrinsic factors such as body mass, sex (Hindell et al. 1991; Kato et al. 2008) and breeding stage (Shaffer et al. 2003). As seen before, marine food resources are scarce and often patchily distributed (Weimerskirch et al. 2007), with this, clutches of a single egg and the development pattern of chicks, predominantly the prolonged nestling period resulting from slow growth, and the large accumulation of fat, are among some of the adaptations to such an unpredictable environments (Boersma & Parrish 1998). Foraging behaviour and flexibility in the diet is particularly important, as it allows individuals to exploit shifting prey diversity and adjust to changing spatio-temporal distributions of prey (Bowen et al. 2006; Montevecchi et al. 2009). Although studies focusing on seabirds during the last decades have multiplied immensely, the vast majority of this work has been focused on breeding individuals (Votier et al. 2011). This tendency is due to the fact that breeders represent an important part of the population and are more likely to return to the colony, increasing the chances for logger retrieval. Seabirds have a long life spans and an extensive period of immaturity (Burger & Shaffer 2008) corresponding up to 50% of the non-breeding adults of the population (Klomp & Furness 1992). Generally these non-breeders attend the colonies along with the breeders for most, if not all the breeding season, but these inexperienced and failed breeders are not necessarily forced as central place foragers since they have no duties at the colony/nest. Therefore the prospect to adapt a more explorative foraging behaviour at sea and rely on different areas than the rest of the population is then possible. Immature individuals normally show higher dispersal rates when compared with breeders (Huyvaert & Anderson 2004) and it’s generally believed that the lower breeding success of younger birds is at least partially associated to lower foraging success (Forslund & Pärt 1995), but there are very few studies which compare the foraging efficiency of experienced and inexperienced individuals (Weimerskirch et al. 2005a).

However, there is no golden rule to such tendencies. Some exceptions have been observed, showing that young inexperienced wandering albatrosses (*Diomedae exulans*) had similar foraging success when compared to experienced adults, differing only on their foraging strategies (Weimerskirch et al. 2005b). Some exceptions include the aforementioned study, which found that young, inexperienced wandering albatrosses (*Diomedae exulans*) actually had similar foraging success to that of experienced adults, but differed in their strategies. Inexperienced birds foraged more intensively and found more prey during the night. In another study by Bunce et al. (2005) on Australasian gannets (*Morus serrator*), it was interestingly found that inexperienced breeders had lower breeding success only when food availability was scarce, though this was not evident in a later and perhaps more detailed work on the same species (Pyk et al. 2007). Other studies show that immature gannets (*Morus bassanus*) breeding on the British Isles, (Votier et al. 2011) can disperse widely, potentially exploring other colonies, but mainly acted as central place foragers when compared with experienced breeders. While first time breeders of black-browed albatross (*Talassarche melanophrys*) had lower reproductive success and lower survival rates when compared with older, more experienced individuals (Nevoux et al. 2007). With such disperse results, it is believed that foraging efficiency develops and increases with age and experience (Zimmer et al. 2011; Le Vaillant et al. 2013; Gutowsky et al. 2014), possibly leading to the notion that some species have such an extended period of immaturity that they are efficient foragers by the time they start breeding (Weimerskirch et al. 2005a; Weimerskirch et al. 2014).

## 1.7 Foraging sexual segregation

Segregation of males and females is particularly common in marine central place foragers during the breeding period, when foraging ranges are restricted by the need to return repeatedly to the breeding site to care for offspring (Page et al. 2005, Weimerskirch et al. 2009). Sexual segregation is thought to reveal competitive exclusion by the dominant sex, or to reflect niche specialisation (Phillips et al. 2004) but could also be a consequence of differing parental roles (Thaxter et al. 2009, Elliott et al. 2010) or differences in the nutritional requirements of males and females as proposed by Lewis et al. (2002). Many studies show that males and females exploit different prey species or habitats, reflecting in between-sex differences in isotopic signatures (Bearhop et al. 2006, Phillips et al. 2011).

Foraging segregation can occur at various spatial scales, ranging from differences in local habitat use to broad geographical distributions (Catry et al. 2005). A recent study by Cleasby et al. (2015) provides clear evidence of sexual segregation in northern gannets (*Morus bassanus*), where males and females differed in their usage of mixed and stratified waters, proving sex-specific habitat segregation across tidal mixing regimes. Other sexual differences in the foraging behaviour of seabirds are often related to sexual size dimorphism found in many species such as the giant petrels (*Macronectes spp*; Gonzáles-Solís et al. 2000) Wandering Albatross (*Diomedea exulans*; Weimerskirch et al. 1993; Weimerskirch 1995) and Gray-headed Albatross (*T. chrysostoma*; Phillips et al. 2004). In some seabirds, sexual dimorphism in body mass and wing morphology is thought to play a functional role in flight performance and is used to explain differences in distribution of males and females at sea at least for part of the year (Phillips et al 2004). However, sexual differences in size and shape may be poor predictors of differentiation in the way male and female seabirds exploit the marine environment. In some species with considerable sexual dimorphism, such as the Cory's Shearwater (*Calonectris borealis*) recent studies show that pronounced sexual size dimorphism in bill size, body mass and wing-length has no apparent connection to foraging behaviour and feeding ecology, at least during the stage of incubation (Navarro et al. 2009; Ramos et al. 2009). Therefore inspecting other stages of this species life cycle, is necessary to understand if sexual segregation and sexual behaviour is due to sexual dimorphism or environmental factors such as food resources. Moreover, the influence of sex on the feeding ecology of seabirds may also be related with the experience of the individual, and, in this study we try also to relate these two variables, sex and breeding experience, in describing the foraging ecology of the birds.

### 1.8 Study questions

We deployed GPS-loggers in male and female (also inexperienced and experienced) Cory's shearwaters during September of 2010 – 2014 (i.e. mid chick-rearing period), in order to disentangle possible intersexual segregation on the foraging strategies, at-sea distribution and trophic ecology of this species. We specifically wanted to answer a three-fold question: (1) Do female Cory's shearwaters differ from males in their foraging strategies and distribution? Until now, most studies reported the inexistence of inter-sexual differences (e.g. Navarro & González-Sólis 2009, Paiva et al. 2010a, but see Ramos et al. 2009 and Navarro et al. 2009 for a counterpoint), especially during the chick-rearing phase when the task of provisioning the growing chick is equally shared between sexes; (2) Will both sexes react differently to life history trait factors, such as environmental stochasticity and breeding experience? We expect females to react more obviously to annual changes of productivity in the colony surroundings, and thus exploit more pelagic waters, like they do during the pre-laying exodus when they segregate from males (Paiva et a. 2013a, Haug et al. 2015). Moreover, inexperienced individuals should exhibit higher values on foraging effort parameters (e.g. maximum distance to colony), especially during years of poor productivity on the colony surroundings (Haug et al. 2015); (3) Will the inter-sexual foraging segregation translate into isotopic segregation and differential body condition between sexes? In this species, like for other marine predators, spatial segregation usually leads to isotopic segregation, through the exploitation of different baseline isoscapes (Graham et al. 2010), through the choice of feeding on isotopically different prey species (Paiva et al. 2010b) or a combination of both. A higher foraging effort usually results into lower adult body condition and overall breeding success (Paiva et al. 2013a).

# Chapter 2 - Methods

## 2.1 Study Area

### 2.1.1 Berlengas archipelago

The Berlengas archipelago is located in the Portuguese coast, at approximately 10Km west of the town of Peniche, in the north Atlantic. The largest Island of the archipelago is the granitic skerry called Berlenga Island (39°12’40’’49N, 09°30’29’’W), that reaches an altitude of 88m, with a maximum length of 1,5Km and a total area of 78,8ha. Two groups of smaller Islets called Estelas and Farilhões are also part of the archipelago and, together with Berlenga, are the three main dry land extensions of the area. The archipelago reached the status of natural reserve in 1981 by the Portuguese government and since then, the islands passed through successive improvements on total area covered and conservation importance, which culminated in June 28th 2011, when the Berlengas Natural Reserve (R.N.B.) was included in the World Network of Biosphere Reserves (W.N.B.R.), under positive ruling of UNESCO (Santos et al. 2012).

The entire archipelago presents high biodiversity, with 76 fish species currently reported in the reserve area (Rodrigues et al. 2008). This, allied with the favourable combination of bathymetric features and ocean and wind circulation (namely the Azorean anti-cyclone and the Portuguese continental shelf upwelling), characterizes the area as rich feeding and breeding grounds for several seabird species (Paiva et al. 2010b; Werner 2010). Berlenga features the only breeding populations of pelagic seabirds in continental Portugal: the Cory’s Shearwater (*Calonectris borealis*), and the Madeira Storm-Petrel (*Oceanodroma castro*), the former only in Farilhões. Presently, the archipelago hosts approximately 850 breeding pairs of Cory’s Shearwaters, distributed among Farilhões Islets (500-550 pairs) and Berlenga Island (300 pairs) (Lecoq et al. 2011). The European Shag (*Phalacrorax aristotelis*), Lesser Black-backed Gull *Larus fuscus*, and until recently, the critically endangered Common Murre *Uria aalgae* also attended breeders on the island.  The most abundant bird is the Yellow-legged Gull (*Larus michahellis*) which possibly undertakes a negative effect on the other seabird populations as stated by Lecoq et al. (2011) when they registered predation of Cory's shearwater eggs at Farilhões islets. Other limiting factors for the presence of seabirds on Berlenga Island are the introduced mammals: Black rats, *Rattus rattus*, and wild rabbits, *Oryctolagus cuniculu*s (Amado 2007). It is known that the presence of rats and other introduced mammals can lead to the decrease of population numbers or even to the extinction of other species including seabirds (Towns et al. 2006; Jones et al. 2008). The archipelago is not only an important breeding ground but its marine area is also important during spring (March) and autumn (September) migrations of the Northern gannet, *Morus bassanus*, which is regularly seen in flocks of several thousand individuals. There are also observations of a Critically Endangered species, Balearic shearwater, *Puffinus mauretanicus*, in large flocks passing near Cape Carvoeiro (Ramirez et al. 2008).

In 2011, the Berlengas Natura 2000 site (SPA) was enlarged to include a significant proportion of its marine area. Linked to this site extension, the Portuguese nature conservation agency (ICNF) launched an initiative to develop a management plan for the new area. Unfortunately, the baseline information proved to be insufficient and clear planned actions were lacking. As a result, the LIFE + Berlengas, launched on June 1st with a total duration of four years was created, coordinated by the Portuguese Society for the Study of Birds (SPEA), in partnership with the Conservation Institute for Nature and Forest (ICNF), the Municipality of Peniche (CMP), the Faculty of Social Sciences and Humanities (FCSH) of the Universidade Nova de Lisboa and with an external observer the School of Tourism and Maritime Technology (ESTM), the Polytechnic Institute of Leiria.

LIFE Berlengas aims to monitor the fauna and flora of the archipelago, control and eradicate invasive species of plants and mammals and implement a sustainable management strategy of natural values, contributing to the conservation of a vast area that includes the Natura 2000 network. Management of seabirds also take place, as monitoring the breeding seabird species (Cory's shearwater, Madeira Storm petrel, Cormorant among others) as well as augmenting the number of artificial nests for Cory's shearwater and storm-petrel, individual tracking of species and metal ringing of these birds, are also included in this project. (http://berlengas.eu/pt/enquadramento).

### 2.1.2 The Atlantic Ocean

When studying top marine predators such as the Cory's Shearwater, the study area is greatly enlarged since most of the tracking data from their migratory processes extends the surrounding colony area to cover large portions of the Atlantic Ocean, as individuals are often present in coastal areas of the North and South America as well as the African coast. Oceanographic characteristics over such large areas are under influence of several environmental factors, showing remarkable variations in ecological aspects, such as sea surface temperature and marine productivity which, in turn, can play a significant role in species distribution and behaviour (Warham 1996; Louzao et al. 2006; Paiva et al. 2010c).

The North Atlantic Basin is under influence of the North Atlantic Gyre, one of the five major oceanic gyres. It is a circular system of ocean currents that stretches across the North Atlantic from near the equator almost to Iceland, and from the east coast of North America to the west coasts of Europe and Africa. The composing currents of the North Atlantic Gyre include the Gulf Stream in the west, the Canary Current in the east, the North Atlantic Current in the north and finally the Atlantic North Equatorial Current in the south, forming a clockwise rotating subtropical gyre (Barton 2001).

This gyre is particularly important for the central role it plays in the thermohaline circulation, bringing salty water west from the Mediterranean Sea and then north to form the North Atlantic Deep Water, as well as nutrient-poor warm water extracted from subtropical areas by the Gulf Stream, and nutrient-rich cold water injected into the system via the Arctic Labrador Current (Barton 2001). This cycling profile is not the same throughout the year, with seasonal variations occurring during summer. This effect is caused by the increase of the sea surface temperature (SST), and results in a significant shift of productivity values of areas close to the Portuguese coast towards areas located in the Arctic Circle (Paiva et al. 2010b; Soares 2013). Consequences such effects on the at-sea distribution and behaviour of Cory’s Shearwater in the North Atlantic can be found throughout the literature (e.g. Granadeiro et al. 1998; Paiva 2009; Roscales et al. 2011), although it’s generally focused on the breeding period.

## 2.2 Study Species

The Cory’s Shearwater (*Calonectris borealis*) is a colonial, medium sized long-distance migrant procellariform. Like most other Procellariiformes, they show no sexual dimorphism in plumage characters, however, sexual dimorphism in bill size and shape, wing length, and overall body size is considerable. Nevertheless, accurately sexing a bird by analysing a single morphometric variable has shown to be almost impossible (Granadeiro 1993, Thibault et al. 1997, Navarro et al. 2009). Until very recently (2014), we could consider two subspecies, Scopoli's shearwater and Cory's shearwater (the Mediterranean *Calonectris diomedea diomedea*, and the Atlantic *Calonectris diomedea borealis* respectively), that are now split into two distinct species following Del Hoyo et al. 2014 (http://www.birdlife.org/). They are nocturnal on their breeding grounds, and in late afternoon birds can be observed waiting for darkness at sea in front of their colonies, in flocks of hundreds or thousands of individuals, before coming onshore (Warham 1990).

*C. borealis* migrates through long trans-equatorial migration routes to move between non-breeding and breeding areas. During the non-breeding season (December-February) they migrate to productive areas located in the South Atlantic which are associated with the Benguela, Agulhas, Brazil and Canary Currents (González-Solis et al. 2007; Ramos et al. 2012). During the breeding season (March-October) Cory’s shearwater migrate and breed in the North Atlantic archipelagos such as Berlengas, Azores, Madeira and Canary archipelagos (Navarro et al. 2007; Paiva et al. 2010b).

Their reproductive behaviour is characterized by a great energetic investment from both parents, spread throughout the 8 months of the breeding cycle, with a long egg incubation period (54 days) and a very long chick rearing period (90 days). During this period, the parents take alternate foraging trips to provide food for the young and restock their own nutritional necessities, often travelling tens to hundreds of kilometres from the breeding site on a single journey (Magalhães 2008). Their food regime consists mainly on epi - and -mesopelagic fish and also on squid (Granadeiro et al. 1998; Xavier et al. 2011).

At the start of the breeding season – pre-laying period - Cory's shearwaters begin to attend their nesting colony around one month prior to laying. These birds present high levels of philopatry, and thus tend to maintain the same nest of previous years, and couples are also usually faithful for life. Males will arrive first and attend the colony more frequently than females, partly in order to protect the selected nest against other conspecifics and copulate. Thereafter they leave the nesting area to feed, replacing the energy lost during migration from the non-breeding areas and stocking up on nutritional reserves that will sustain them through the early stages of the reproductive process (Werner 2010, Paiva et al. 2013a).

Females embark on an approximate twenty day journey (Jouanin et al. 2001) a pre-laying exodus after copulation, key to build up body reserves to form and lay their egg. This departure starts in early May and after their return to the colony, in late May, females lay the egg which will be incubated in shifts by the breeding pair during almost two months (Paiva et al. 2010b). This dual effort of biparental care also extends to the high energy demand period of chick-rearing, after the eggs are hatched (starting at the end of July). To respond to these high energetic needs, the foraging strategy employed by the species is based on a cycle between short (1-2 days) and long trips (3-9 days), with short trips used to provide for the chick, while long trips are performed to replenish the adult’s nutritional reserves. (Magalhães et al. 2008; Navarro and González-Solís 2009; Paiva et al. 2010a; 2010b; 2010c). This strategy allows birds to balance the constraint of regularly visiting the colony on the one hand, and accessing better fishing areas farther from the colony on the other.

As the chick rearing process progresses, both the frequency of food input and degree of digestion by the parents decrease (Ramos et al. 2003). By the end of September, the chick will stop growing and a reduction in the overall body size will be compensated by wing growth. This process lasts until late October and early November when chicks finally fledge to start exploring the ocean at night (Warham 1990). During winter, the species travels thousands of kilometres to feed in warmer climates, being found mainly in South Africa, Brazil, and southern central Atlantic (Camphuysen & Van Der Meer 2001; Ramos et al. 2009b)

## 2.3 Fieldwork

The tracking study was conducted on Berlenga Island located in the Portuguese coast (39° 23’ N, 9° 36’ W), during September (chick-rearing period data) of 2010 – 2014. GPS tracking devices CatTraq Travel Loggers (Fig. 1) (Perthold Engineering LLC) were employed as GPS-loggers, as these gadgets seem to provide the most accurate data, with an error of meters (Ramirez et al. 2008). This specific device (44.5 * 28.5 * 13mm) weighs 15g and contains a SiRF StarIII chipset, a patch antenna and an 180mAh Lithium-ion battery. Devices were stripped of their original plastic case and sealed with a thermoretractile rubber sleeve for waterproofing. Loggers weight represented between 1.9% and 2.7% (median = 2.5%) of the birds weight.

Devices were set to record data each 5 minutes, with loggers' batteries draining out in about 15 days. The study colony is situated on the eastern side of the "Old Island" of Berlenga where approximately 130 pairs of Cory's shearwater nest in rock crevices, burrows and (mostly) artificial nests.

**Figure 1** - GPS tracking devices, CatTraq Travel Loggers employed as GPS-loggers.

Birds were captured during the night at their nest sites, weighed and individually identified by their ring numbers. GPS loggers were then attached using TESA® tape (Wilson et al. 1997) to the contour feathers along and in between both scapula's (Fig. 2). As an extra security measure we glued the tips of each tape stripe used to attach the logger. The birds were then returned to their nests, this process took less than 10 minutes in order to minimize the overall stress. At logger retrieval, a blood sample (Fig. 2) of about 0.5 ml was collected from the tarsal vein of each individual, for evaluation of its trophic choices during the tracking period, through stable isotope analysis (SIA; trophic ecology).

The 55 tracked birds (N = 27 female and N = 28 male Cory's shearwaters) were divided into experienced and inexperienced individuals using the total number of breeding attempts as a proxy for experience, following indications of previous studies (Jones & Ryan 2014; Froy et al. 2015; Haug et al. 2015) and the prediction that reproductive success typically increases with breeding age and experience in seabirds (e.g. Forslund and Pärt 1995). Our study benefited from a long-term database of the breeding population, such that minimum age, sex and previous breeding experience (i.e. fledging success) were known for most of the individuals (Lecoq et al. 2011).

**Figure 2 -** Fieldwork procedures at the breeding colony (A) Process of logger deployment; (B) Collection of blood samples.

Thus, birds included in this study were categorized as inexperienced (≤ 2 years of breeding successfully; N = 26) and experienced (> 2 successful years; N = 29) individuals, based on the frequency distribution of the historical breeding success records. The breeding scores extended back to 2005 for our study site, and we considered the 7-year breeding success of the individuals, prior to our study (2005–2010). The former assumption is supported by a positive significant correlation (Spearman $r_s = 0.77$, $N = 55$, $P < 0.001$) between estimated age of individuals and chicks that fledged by each individual per breeding attempt since 2005.

Each year, the tracked birds were measured (body weight and wing length) in order to calculate their body condition index (BCI). This index was obtained from the residuals of the linear regression of body weight on wing length, a measure of structural size (Brown 1996). BCI is therefore a measure of mass corrected for size and is considered an indicator of energetic reserves.

### 2.4 Area of Restricted Search (ARS) zones

Fauchald & Tveraa (2003) developed a technique, named First Passage Time (FPT) to assess the spatial scale that animals use to encounter their prey. FPT is, by definition, the time required for an animal to pass through a circle with a given radius r. By moving this circle along the path of the animal, we will obtain a scale-dependent measure of search effort and therefore the behavioural response of an individual in the environment. Because top marine predators usually forage in a patchy and hierarchical environment (Fauchald 1999), increases in the turning rate and/or decreases in speed of its foraging path should be related to the so-called Area Restricted Search (ARS) behaviour. ARS will then appear as an individual reaction to changes in the resources availability and distribution, by increasing the residence time in the productive patch (Fauchald & Tveraa 2003).

Zones of Area Restricted Search (ARS) were estimated applying First Passage Time (FPT) analysis, following (Fauchald & Tveraa 2003) and using software R 3.0 (R Development Core Team 2014). Usually, ‘in water’ positions result in very small-scale ARS zones (<100 m diameter), which considerably increase the variance in FPT and can camouflage larger-scale ARS zone (Weimerskirch et al. 2007). To address this problem, we removed bouts on the water and interpolated locations to obtain a distance interval of 0.1 km for FPT analysis (Pinaud 2008). We considered positions with speed < 3 km $h^{-1}$ as resting or preening behaviours on the water or inland, after inspection of the frequency distribution of speeds. Following the recommendations of (Pinaud 2008), FPT analysis was performed in two steps: 1) to detect large-scale ARS we run the analysis on the whole path, estimating the FPT every 1 km for a radius *r* from 1 to 50 km; 2) to detect small spatial scale events we run again FPT analysis every 0.1 km for an *r* varying between 0.1 and 10 km. The plot representing variance in log (FPT) as a function of *r* allowed us to identify the ARS scales by peaks in the variance. In this calculation, FPT was log transformed to make the variance independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003). It is also possible to locate where the bird entered an ARS zone and the time spent on that area by plotting FPT values where a peak of variance occurred as a function of time since departure from the colony. ARS locations were also used to feed the General Linear Additive Models (GAMMs).

### 2.5 Habitat use

GPS locations of each bird where ARS behaviour was detected (ARS zones) were examined under the *adehabitatHR* R package (Calenge 2006) generating Kernel Utilization Distribution (Kernel UD) estimates. The most appropriate smoothing parameter (h) was chosen via least squares cross-validation for the unsmoothed GPS data, and then applied as standard for the other datasets and grid size was set at 0.05º (to match the grid of environmental predictors). We considered the 50% and 95% kernel UD contours to represent the core foraging areas (FR) and the home range (HR), respectively.

The extent of within-year overlap between male and female home ranges was estimated using Bhattacharyya's affinity (BA; Bhattacharyya 1943), which ranges from 0 (no overlap) to 1 (complete overlap). Using BA as a measure of spatial overlap, we used a randomization technique to test the null hypothesis that there was no difference in the spatial distribution of males and females in each year of the study. If the null hypothesis was true, the magnitude of the overlap between males and female 50% and 95% kernels should not differ significantly from that calculated if sex were randomly assigned. Therefore, for each year the sex of each bird was randomly assigned using the same sex ratio as the observations in that year. In total, we generated a null distribution for BA based on 1000 randomizations of our dataset in order to test whether the overlap between male and female home-ranges was significantly different than expected. P-values were determined by the proportion of random overlaps that were smaller than the observed overlap, if the observed overlap was smaller than all 1000 randomly generated overlaps, then p was ≤ 0.005 (see Breed et al. 2006 for a similar approach). More details on BA and other measures of spatial overlap can be found in Fieberg & Kochanny (2005).

### 2.6 Environmental data

The extended winter North Atlantic Oscillation (NAO) index was used as a large-scale environmental predictor for the North Atlantic area, and specifically for the Western Iberia Upwelling Ecosystem (WIUE). The NAO index refers to a north–south alternation in atmospheric mass between the subtropical Atlantic and the Arctic, and thus involves out-of-phase behaviour between the climatological low-pressure centre near Iceland and the high-pressure centre near the Azores (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based). We also used some small-scale environmental predictors, such as chlorophyll *a* concentration (CHL) and SST data, downloaded from http://oceanocolor.gsfc.nasa.gov/, as daily night-time products with a resolution of 0.04° (approx. 4 km) in the SMI-HDF format. Bathymetric data (BAT), taken as water depth, was downloaded from the ETOPO2v2 database at a spatial resolution of 0.03° (approximately 3 km; http://www.ngdc.noaa.gov/mgg/fliers/01mgg04.html). HDF files were converted to raster using the Marine Geospatial Ecology Tools in ArcGIS 9.2 (Roberts et al. 2010), and then to ASCII to create composites. All composites were constructed using the freeware R environment (version 2.14, R Core Team 2014) and *mosaic* function of the *raster* package. Spatial gradients of SST, CHL and BAT (SSTG, CHLG and BATG, respectively) were obtained by estimating the proportional change (PC) within a surrounding 3 × 3 cell grid using a moving window as follows: PC = [(maximum value − minimum value) × 100/maximum value] (Louzao et al. 2006). SSTG and CHLG are believed to be good indicators of oceanic fronts, while the BATG was used as a proxy for slope. Additionally, two more static variables were generated. Distance to land (DLAN) was calculated using the *distance* tool in the ArcGIS 10.1 *spatial analyst* toolbox.

## 2.7 Stable isotope analysis (SIA)

Stable-nitrogen isotope ratios ($^{15}N$: $^{14}N$, expressed as $\delta^{15}N$) and stable-carbon isotope ratios ($^{13}C$: $^{12}C$, expressed as $\delta^{13}C$) on plasma and red blood cells of Cory's shearwater were assessed to investigate the effect of experience on their foraging ecology and prey selection. The ratios represent the prey ingested in the past few weeks before the blood sample. The $\delta^{15}N$ is mainly used to define the trophic position of the consumer, while $\delta^{13}C$ reflects the foraging habitat of the consumer (Inger & Bearhop 2008, Ceia et al. 2012). It is assumed that potential intraspecific differences in assimilation efficiency or physiology, does not impact the blood isotope values significantly (Votier et al. 2011). There is a gradient of high to low values of $\delta^{13}C$ from coast to offshore due to the organic enrichment at the coast that is gradually diluted. Red blood cells (RBC) are regenerated every 12-22 days while plasma has a turnover rate of about 7 days, therefore they represent prey ingestion in different time scopes: RBC reflects the trophic ecology the last few weeks, and plasma reflects choices made in the last trips before sampling (i.e. around 7 days; Inger & Bearhop 2008).

Each of the tracked birds was sampled upon return from a foraging trip. Blood samples (1 ml) were collected from the tarsal or brachial vein using 25-gauge needles under license. Blood samples were then separated into plasma and red blood cells (hereafter termed RBC) by a centrifugation at 12000 rpm for 15 min, within 2-4 hours of sampling and stored frozen at –20 °C until preparation for analysis. Successive rinses with a 2:1 chloroform/methanol solution were performed on the plasma samples in order to deplete it for lipids, which may disturb the results (Cherel et al. 2005b). Plasma samples were dried in an aspirating hood for 48h at 60°C for the ethanol to evaporate. Isotope ratios of carbon and nitrogen were then determined through standard methodology (Bearhop et al. 2006, Phillips et al. 2009) by continuous-flow isotope ratio mass spectrometry, using an EA-IRMS (Isoprime, Micromass, UK). The analytical precision for the measurement was 0.2‰ for both carbon and nitrogen. All values presented are means ± 1 SD unless otherwise stated.

### 2.8 Statistical analysis

Generalized Linear Mixed Models (GLMMs) tested the effect of (1) year (2010 – 2014), (2) sex and, (3) the interaction between 1 and 2 (i.e. independent variables) on the (1) regional and (2) local environmental predictors, (3) foraging trip characteristics, (4) habitat of foraging areas, (5) trophic ecology and (6) fitness parameters (i.e. dependent variables). Trip identity was nested within the individual as a random term to avoid potential pseudo-replication problems, since all individual birds performed multiple trips. Gaussian distribution of error terms and a log-link function were used in the modelling. Post-hoc multiple comparisons with Bonferroni correction were used to identify significant differences between categories of each independent variable. R packages used in the GLMMs were *lme4* (Bates et al. 2014) and *lmerTest* (Kuznetsova et al. 2014).

When modelling the occurrence of ARS behaviour (First Passage Time – FPT – duration) in male and female Cory's shearwaters we used GAMMs to (1) select the most parsimonious models explaining FPT and (2) estimate smoothers for each of the environmental parameters for the top-ranked models ($\Delta$AICc < 2). GAMMs combine the utilities of linear mixed models (Pinheiro &

Bates 2000) and generalized additive models (Hastie & Tibshirani 1990) so that random factors, fixed factors and nonlinear predictor variables can all be estimated in the same statistical model. We developed separate models for male and female birds and included (1) year, (2) breeding experience and (3) all different environmental predictors of productivity (e.g. SST) as fixed factors, trip identity within bird identity as a random term (to account for pseudoreplication issues).

As part of the gam functions within the R package *mgcv* (Wood 2002) the smoothing parameter is chosen automatically using generalised cross-validation (GCV). In order to model spatial auto-correlation we included an isotropic thin plate spline which is set up as a two-dimensional smoother based on both x and y coordinates (in R this would be specified as s(x,y)). Incorporating a spatial smoother is one means of modelling a spatial trend within a model, more details on this approach can be found in Wood (2002). Prior to modelling we examined correlations between all environmental variables in order to ascertain whether collinearity may have occurred. We assumed that a correlation of greater than Spearman correlation: $r_s = 0.5$ was problematic, and thus the environmental predictor (from the pair of highly correlated ones) which produced the highest Akaike Information Criteria (AIC) value on a univariate analysis was excluded. Initially we restricted GAMMs to a maximum of 5 knots to prevent over-fitting, however if GAMMs failed diagnostic checks we increased the number of knots until these checks were satisfactory. For the spatial smoothers in the models we used the default settings in the *mgcv* package (Wood 2002) to estimate the number of knots required. When performing GAMMs, minimum adequate models were selected by backwards selection, using *K*-fold cross-validation, where *K* = 5, following Hastie & Tibshirani (1990).

To establish the isotopic niche among periods with the stable isotope data we applied the recent metric SIBER (Stable Isotope Bayesian Ellipses in R), which is based in a Bayesian framework that confers a robust comparison to be made among data sets concerning different sample sizes (Jackson et al. 2011). The area of the standard ellipse (SEAc, an ellipse that has 40% probability of containing a subsequently sampled datum) was adopted to compare between inexperienced and experienced bird isotopic signatures and their overlap in relation to the total niche width (both groups combined), and a Bayesian estimate of the standard ellipse and its area ($SEA_B$) to test whether group 1 is smaller than group 2 (i.e. *p*, the proportion of ellipses in inexperienced birds that were lower than in experienced individuals; see Jackson et al. 2011 for more details). All the metrics were calculated using *standard.ellipse* and *convexhull* functions from SIBER implemented in the package SIAR (Stable Isotope Analysis in R; Parnell et al. 2010) under R 2.15.2 (Core Team 2014). All data are presented as mean ± 1 SD, unless otherwise stated. Results were considered significant at $p \leq 0.05$.

# Chapter 3 - Results

## 3 Results

During 2010, 2011 and 2013 the NAO index (Jun - Aug) was on average 5.7 values significantly lower and the SST within 200km off Berlenga was 2.8 ºC significantly higher when compared to 2012 and 2014. During the same 3 years, birds travelled ~ 187.3 km significantly further from their colony and spent more 14.1 % of time in foraging areas when compared to 2012 and 2014. Moreover, females travelled ~101.8 km significantly further from their colony and spent more 18.5 % of time in foraging areas when compared to male Cory's shearwaters (Table I and II, Fig. 3). SST and ASST were on average 3.2 and 4.1 ºC significantly higher, respectively, in 2010, 2011 and 2013 than in 2012 and 2014, while CHLA was 1.1 $mgm^{-3}$ lower on 2010 when compared to the other four years. The plasma carbon and nitrogen signatures were 2.1 and 1.5 ‰ significantly lower and higher, respectively, in the years 2010, 2011, 2014 than in 2012 and 2013. Females showed a plasma nitrogen signature 2.1 ‰ lower and a plasma SEAb 1.2 units higher than males. The adult's BCI was 0.6 significantly lower in 2010, 2011, 2013 than in 2012, and 2014, while females had a 0.7 lower BCI than males.

During 2010, 2011 and 2013 there was a significantly smaller proportion of overlaps between sexes for both the 50% and the 95% Kernel UD. During 2012 and 2014, the percentage of overlap between sexes was high (>42.8%) and non-significantly different (Table III).

**Table I.** Mean (±SD) regional and local environmental predictors in the colony surroundings of female and male Cory's shearwaters from Berlenga between 2010 and 2014; foraging trip characteristics, habitat of foraging areas, trophic ecology and fitness parameters of both sexes. Extended winter (december-march) North Atlantic Oscillation (NAO) index according to Hurrel 1995 (https://climatedataguide.ucar.edu/ climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based). FA – core Foraging Area; 50% Kernel Utilization Distribution (50 UD). Environmental predictors are for summer (June-September) of each year, unless otherwise stated. SEAb - Bayesian approximation of the standard ellipse area (see Jackson et al. 2011 for more details on these metrics of isotopic niche width). Values are mean ± SD.

| | **2010** | | **2011** | | **2012** | | **2013** | | **2014** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **female** | **male** | **female** | **male** | **female** | **male** | **female** | **male** | **female** | **male** |
| **Regional environmental predictors** | | | | | | | | | | |
| Extended winter NAO index (Dec - Mar) | -4.6 | | -1.6 | | 3.2 | | -2.0 | | 3.1 | |
| NAO index (Jun – Sep) | -2.3±0.5 | | -1.2±0.3 | | 1.65±0.2 | | -1.5±0.4 | | 1.3±0.4 | |
| **Local environmental predictors (within 200 km)** | | | | | | | | | | |
| Chlorophyll *a* concentration (CHLA; mg m$^{-3}$) | 0.6±0.2 | | 1.7±0.3 | | 2.1±0.1 | | 1.3±0.5 | | 2.3±0.3 | |
| Sea Surface Temperature (SST; ºC) | 21.9±0.7 | | 20.0±1.5 | | 17.2±1.8 | | 19.2±1.4 | | 16.9±1.5 | |
| SST anomaly | 1.8±0.3 | | 0.9±0.2 | | -1.1±0.4 | | 0.7±0.2 | | -0.9±0.2 | |
| **Foraging trip characteristics** | | | | | | | | | | |
| N tracks [N birds] | 69 [10] | 50 [9] | 19 [5] | 21 [6] | 34 [4] | 40 [5] | 22 [5] | 20 [4] | 15 [3] | 16 [4] |
| Maximum distance from colony (km) | 823.2±43.1 | 587.5±54.4 | 624.2±67.1 | 342.6±67.1 | 194.4±32.1 | 179.1±44.0 | 542.9±87.3 | 209.1±66.9 | 98.1±22.1 | 134.3±22.2 |
| Time spent flying trip$^{-1}$ day$^{-1}$(h) | 8.6±1.1 | 6.1±1.0 | 6.6±1.4 | 5.0±1.3 | 4.9±1.1 | 3.1±1.6 | 6.8±1.2 | 4.8±1.0 | 4.3±1.5 | 3.3±1.9 |
| % of time spent in foraging areas | 45.2±6.7 | 29.9±5.5 | 37.5±6.2 | 29.3±5.0 | 18.9±3.8 | 17.3±3.7 | 38.3±5.8 | 28.7±5.6 | 18.0±2.2 | 18.5±4.4 |
| **Habitat of foraging areas (within FR)** | | | | | | | | | | |
| Chlorophyll *a* concentration (CHLA; mg m$^{-3}$) | 0.5±0.3 | 1.1±0.8 | 0.9±0.4 | 1.4±0.3 | 1.4±0.5 | 1.7±0.3 | 0.7±0.5 | 1.3±0.6 | 1.6±0.7 | 1.9±0.4 |
| Sea Surface Temperature (SST; ºC) | 20.1±0.7 | 18.3±0.9 | 19.7±0.9 | 18.0±0.5 | 17.3±0.7 | 17.1±0.8 | 19.9±0.6 | 18.6±0.2 | 17.8±0.4 | 17.9±0.2 |
| SST anomaly (ASST) | -0.7±0.1 | 1.4±0.6 | -0.9±0.6 | 1.1±0.4 | -2.1±0.4 | -1.8±0.7 | -0.8±0.4 | 1.3±0.5 | -2.3±0.5 | -1.6±0.9 |
| **Trophic ecology** | | | | | | | | | | |
| Plasma carbon signature (‰) | -20.5±0.5 | -18.9±0.7 | -19.1±0.6 | -18.0±0.4 | -18.4±0.6 | -17.9±0.5 | -19.3±0.4 | -18.3±0.5 | -18.4±0.2 | -17.5±0.3 |
| Plasma nitrogen signature (‰) | 13.9±0.4 | 14.4±0.5 | 13.1±0.4 | 14.0±0.3 | 12.8±0.3 | 13.0±0.4 | 13.4±0.3 | 14.1±0.5 | 12.7±0.4 | 13.5±0.5 |
| Plasma SEAb | 1.8 | 1.1 | 1.3 | 0.8 | 0.8 | 0.5 | 1.2 | 0.7 | 0.7 | 0.6 |
| **Fitness parameter** | | | | | | | | | | |
| Adult's body condition index (BCI) | -1.2±0.4 | -0.5±0.2 | -0.9±0.5 | -0.5±0.2 | 0.4±0.5 | 0.7±0.2 | -0.8±0.2 | -0.4±0.3 | 0.5±0.2 | 0.8±0.3 |

**Table II.** Generalized Linear Mixed Effect Models (GLMMs) testing the effect of the interaction between year (2011, 2012 and 2014) and sex (male and female) on regional and local environmental predictors in the colony surroundings (200 km around the breeding colony), foraging habitat and trip characteristics and spatial ecology and fitness parameters shown in Table 1. 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.

| | Year | | | Sex | | | Year*Sex | | |
|---|---|---|---|---|---|---|---|---|---|
| **Variables** | **GLMM** | **P** | **Effect** | **GLMM** | **P** | **Effect** | **GLMM** | **P** | **Effect** |
| **Regional environmental predictors** | | | | | | | | | |
| Extended winter NAO index (December - | — | — | — | — | — | — | — | — | — |
| NAO index (Jun - Aug) | $F_{4,15} = 29.36$ | **< 0.001** | 2010,2011,2013 < 2012,2014 | — | — | — | — | — | — |
| **Local environmental predictors (within 60** | | | | | | | | | |
| Chlorophyll *a* concentration (CHLA; mg $m^{-3}$) | $F_{4,167} = 2.42$ | 0.11 | — | — | — | — | — | — | — |
| Sea Surface Temperature (SST; ºC) | $F_{4,167} = 3.45$ | **0.01** | 2010,2011,2013 >2012,2014 | — | — | — | — | — | — |
| **Foraging trip characteristics** | | | | | | | | | |
| N tracks [N birds] | — | — | — | — | — | — | — | — | — |
| Maximum distance from colony (km) | $F_{9,296} = 2.11$ | **0.03** | 2010,2011,2013 > 2012,2014 | $F_{9,296} = 3.78$ | **0.001** | females > males | $F_{9,296} = 2.09$ | **0.04** | 2010 females |
| Time spent flying $trip^{-1}$ $day^{-1}$(h) | $F_{9,296} = 1.51$ | 0.15 | — | $F_{9,296} = 1.22$ | 0.21 | — | — | — | — |
| % of time spent in foraging areas | $F_{9,296} = 10.02$ | **< 0.001** | 2010,2011,2013 >2012,2014 | $F_{9,296} = 2.00$ | **0.04** | females > males | $F_{9,296} = 1.38$ | 0.19 | — |
| **Habitat of foraging areas (within FR)** | | | | | | | | | |
| Chlorophyll *a* concentration (CHLA; mg $m^{-3}$) | $F_{9,296} = 1.98$ | **0.04** | 2010 < all other years | — | — | — | — | — | — |
| Sea Surface Temperature (SST; ºC) | $F_{9,296} = 3.24$ | **0.001** | 2010, 2011,2013 > 2012,2014 | $F_{9,296} = 1.65$ | 0.11 | — | $F_{9,296} = 1.37$ | 0.21 | — |
| SST anomaly (ASST) | $F_{9,296} = 2.48$ | **0.01** | 2010, 2011,2013 > 2012,2014 | $F_{9,296} = 3.23$ | **0.001** | females < males | $F_{9,296} = 2.22$ | **0.02** | 10, 11,13 F < |
| **Trophic ecology** | | | | | | | | | |
| Plasma carbon signature (‰) | $F_{9,296} = 2.11$ | **0.03** | 2010,2011,2013 < 2012,2014 | $F_{9,296} = 1.59$ | 0.13 | females < males | $F_{9,296} = 1.68$ | 0.11 | — |
| Plasma nitrogen signature (‰) | $F_{9,296} = 2.47$ | **0.01** | 2010,2011,2013 >2012,2014 | $F_{9,296} = 3.32$ | **0.001** | females < males | $F_{9,296} = 2.01$ | **0.04** | 10, 11,13 F < |
| Plasma SEAb | $F_{9,296} = 1.48$ | 0.17 | — | $F_{9,296} = 1.92$ | **0.05** | females > males | $F_{9,296} = 1.40$ | 0.19 | |
| **Fitness parameter** | | | | | | | | | |
| Adult’s body condition index (BCI) | $F_{9,296} = 2.48$ | **0.01** | 2010,2011,2013 < 2012,2014 | $F_{9,296} = 3.25$ | **0.001** | females < males | $F_{9,296} = 2.55$ | **0.01** | 2010 females |

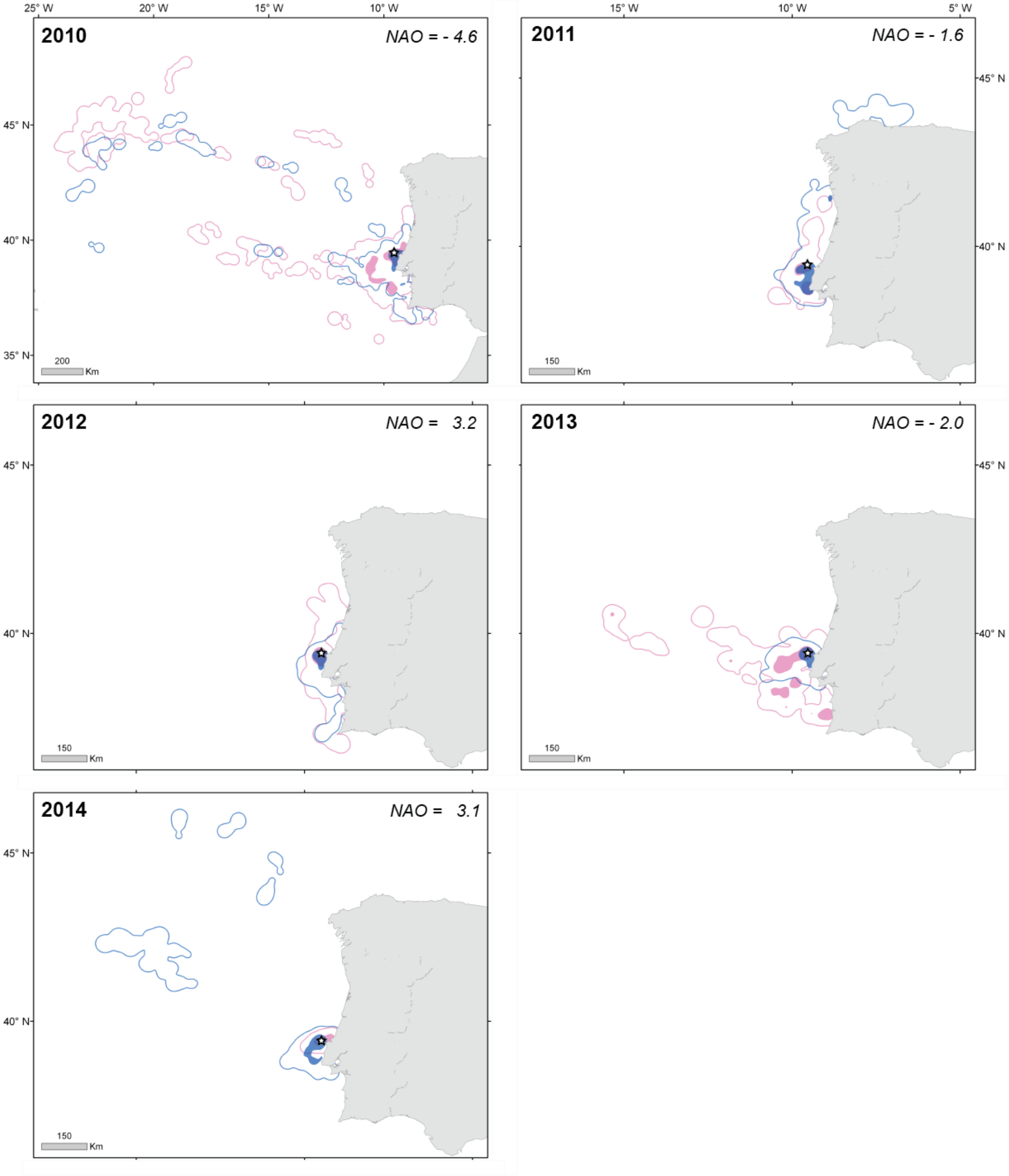

**Figure 3.** Home range (contour lines; 95% kernel UD) and foraging areas (filled areas; 50% kernel UD) of male (blue) and female (pink) Cory's shearwaters during the chick-rearing seasons of 2010-2014. Polygons a) Raw location data; b) kernel density based utilization distributions at 95% (dotted lines) and 50% (solid lines). Bass Rock is shown as a square and the approximate position of the tidal mixing front each year is shown as a solid black line in (b). Also shown at the top-right corner of each map, the value of extended winter (december-march) North Atlantic Oscillation (NAO) index according to Hurrel 1995 (https://climatedataguide.ucar.edu/ climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based).

**Table III.** Estimated overlap (Bhattacharyya's Affinity, BA) between male and female Cory's shearwaters Kernel Utilisation Distributions (Kernel UD). *p* represents the proportion of randomised overlaps that were smaller than the observed overlap

| Kernel UD | Year | % Overlap between sexes | BA | *p* |
|---|---|---|---|---|
| 50% | 2010 | 34.5 | 0.29 | **0.02** |
| | 2011 | 32.4 | 0.31 | **0.01** |
| | 2012 | 42.8 | 0.42 | 0.12 |
| | 2013 | 31.1 | 0.32 | **0.01** |
| | 2014 | 44.6 | 0.49 | 0.15 |
| 95% | 2010 | 56.3 | 0.65 | **0.04** |
| | 2011 | 53.1 | 0.68 | **0.03** |
| | 2012 | 68.2 | 0.76 | 0.11 |
| | 2013 | 50.9 | 0.70 | **0.05** |
| | 2014 | 65.8 | 0.81 | 0.19 |

Overall, our models showed a good predictable capacity, explaining > 22.4% and > 22.7% of the deviance in the FPT duration (proxy of foraging activity) of females and males, respectively (Table IV). The FPT duration in females increased with increasing BAT and BATG and with decreasing distance to land and SST (Fig. 4). Moreover, FPT duration was typically higher in experienced females and with lower SSTA, than in inexperienced females with higher SSTA. The FPT duration was also higher in recent years and in experienced females, than in earlier study years and inexperienced females. FPT duration increased in males, with decreasing BAT and BATG, SST and DLAN, while it increased with increasing CHLG. Also, FPT duration was also higher in recent years and in experienced males, than in earlier study years and inexperienced males (Table IV, Fig. 4).

**Table IV.** Parameter estimates (±SE) from Generalized Additive Mixed Models (GAMMs) fitted to the Area Restricted Search behaviour (i.e. First Passage Time – FPT – duration; proxy of foraging activity) of female and male Cory's shearwaters showing the ranking on the candidate models based on the corrected Akaike Information Criteria (AICc). All evaluated models included individual identity as a random factor. Models are ordered by the AIC value. Presented are the habitat variables in the top-ranked models (**Δ**AICc < 2). ED - Explained deviance (%); BAT – Bathymetry (m); BATG –BAT gradient (%); SST - Sea Surface Temperature (ºC); SSTG –SST gradient (%); CHL – Chlorophyll *a* concentration (mgm$^{-3}$); CHLG – CHL gradient; DLAN – Distance to land (m).

| | **FPT duration in females** | | | | | | **FPT duration in males** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Model structure** | **AICc** | **ΔAICc** | **AICc Wgt** | **ED** | | | **AICc** | **ΔAICc** | **AICc Wgt** | **ED** |
| BAT * BATG + DLAN | 243.8 | 0.01 | 0.79 | 42.1 | | BAT * BATG | 162.3 | 0.07 | 0.64 | 39.2 |
| SST | 302.0 | 1.45 | 0.62 | 35.2 | | SST + DLAN | 199.2 | 1.01 | 0.52 | 30.0 |
| Experience * SSTA | 526.4 | 1.57 | 0.53 | 28.9 | | CHLG | 277.0 | 1.55 | 0.44 | 22.7 |
| Experience * Year | 507.2 | 1.34 | 0.47 | 22.4 | | Experience * Year | 309.7 | 1.76 | 0.39 | 31.2 |
| Constant | 602.9 | 2.15 | 0.11 | 9.1 | | Constant | 528.4 | 2.46 | 0.12 | 10.9 |
| | | | | | | | | | | |
| **Fixed effects** | **β±SE** | **z** | **p** | | | | **β±SE** | **z** | **p** | |
| Intercept | 1.35±0.07 | 19.45 | <0.001 | | | Intercept | -0.94±0.19 | -18.84 | <0.001 | |
| BAT : BATG | 4.23±0.22 | 15.23 | <0.001 | | | BAT : BATG | -7.12±0.14 | 23.12 | <0.001 | |
| DLAN | -1.23±0.09 | 3.15 | 0.10 | | | SST | -4.14±0.23 | -16.23 | <0.001 | |
| SST | -2.65±0.14 | -6.24 | 0.01 | | | DLAN | -2.36±0.11 | -7.12 | 0.01 | |
| Experienced : SSTA | -4.65±0.17 | 14.89 | 0.001 | | | CHLG | 5.24±0.21 | 18.23 | <0.001 | |
| Inexperienced : Year | 6.52±0.42 | 20.14 | <0.001 | | | Inexperienced : Year | 4.12±0.25 | 14.12 | 0.001 | |
| Random intercept for Bird_ID (variance±SD) | 0.10±0.02 | | | | | | 0.15±0.09 | | | |

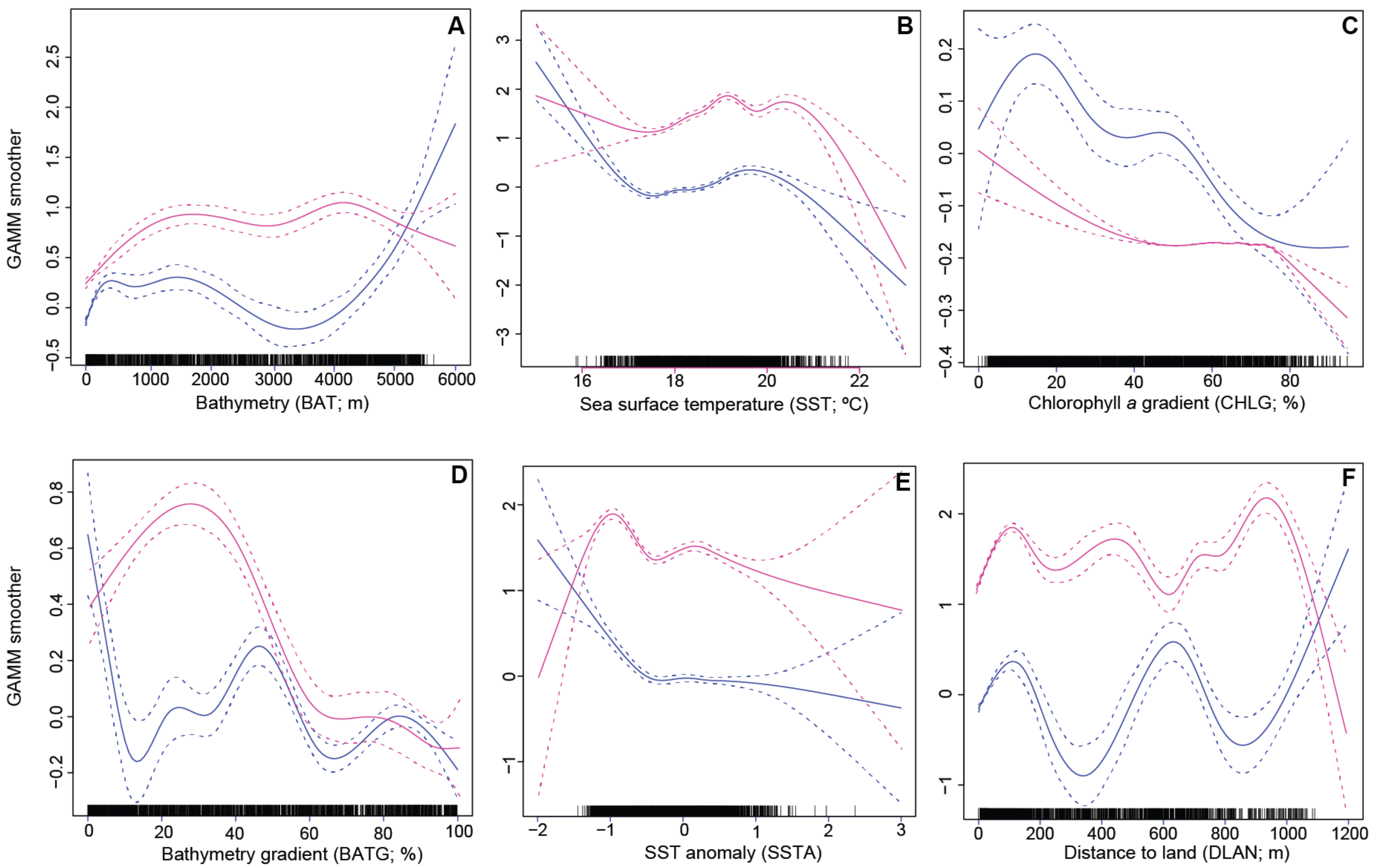

**Figure 4**. Habitat selection functions for (A) bathymetry, (B) sea surface temperature, (C) chlorophyll *a* gradient, (D) bathymetry gradient, (E) sea surface temperature anomaly and (F) distance to land. Plots show the predicted curve from the best models (solid lines) and 95% confidence intervals (dashed lines) for male (blue) and female (pink) Cory's shearwaters. GAMM – Generalized Additive Mixed Model.

# Chapter 4 - Discussion

## 4.1 General discussion

Several studies report partial or complete inter-sexual spatial foraging segregation in seabird species, such as in black-browed albatrosses *Thalassarche melanophris* (Huin 2002), cape gannets *Morus capensis* (Grémillet et al. 2004), Hawaiian petrels *Pterodroma sandwichensis* (Wiley et al. 2012) or streaked shearwaters *Calonectris leucomelas* (Yamamoto et al. 2011). While seeking if inter-sexual segregation occurred in our study species, our results reveal that individual experience as well as sex differences can play a significant role in Cory's Shearwater's ecology and at-sea behaviour during the chick-provisioning season, specially taking into account the changing levels of productivity that occurred in the surroundings of the birds' colony throughout the time frame of our study (2010-2014). As described by former studies (e.g. Paiva et al. 2013a, 2013b; Haug et al. 2015) our results also link the negative NAO index values (Hurrel et al. 1995) and the subsequent decrease in productivity (proxied by a decrease in CHLA and increase in SST) in the Northeast Atlantic with alterations in the foraging behaviour of Cory's Shearwaters breeding in the continental shelf of Portugal.

In fact, there are a number of studies in relating sexual differences with foraging ecology, often with contradictory results. Overall, seabirds with pronounced sexual size dimorphism are often more associated with sexual differences in foraging behaviour and ecology (González-Solís et al. 2000, Phillips et al. 2004). Sex-specific differences in foraging behaviour are usually credited to the influence of body size on foraging efficiency and intra-specific competition but there are also studies showing no sexual differences in foraging ecology and behaviour (Navarro et al. 2009, Ramos et al. 2009). The study presented here shows the importance of examining a large range of environmental conditions, indispensable to detect sexual differences in foraging ecology and behaviour, even if such differences are relatively small. However, even small differences may be ecologically relevant because both sexes will face strong competition when environmental conditions are poor.

According to our first prediction, our study suggests that inter-sexual differences in the foraging behaviour and distribution of Cory's shearwaters do exist. These differences are evident in years of greater stochasticity (specially during 2010, 2011 and 2013, when NAO index values were very low), when females travelled significantly further from their colony and spent more time in foraging areas when compared to male Cory's shearwaters (Table I and II, Fig. 3). Contrastingly during the breeding seasons of 2012 and 2014, no significant differences in foraging areas were observed, leading us to believe that productivity plays an important role in inter-sexual differences in the foraging behaviour of these birds.

On the other hand, and according to our second prediction, life history trait factors such as environmental stochasticity, affected both sexes in different ways. Females exploited more pelagic waters during poor oceanographic productivity while males remained closer to areas surrounding the colony. Interestingly, experience also seems to play an important role on the birds foraging behaviour, as our result show that inexperienced males exhibit higher values on foraging effort parameters (e.g. maximum distance to colony) when compared to more experienced ones. Inexperienced individuals presented a higher pelagic behaviour than experienced ones, with feeding strategy based on prey located on lower trophic levels. Experienced individuals' distribution was greatly concentrated around coastal areas, with few foraging areas and diet based on higher trophic level prey. These results could be explained by the fact that young Cory's shearwaters (non-breeders) spend most of the time at sea, as do many other species of seabirds (Warham 1996). Thus, the opportunity is presented to learn and gather information on the conditions and foraging opportunities of different sites, allowing them to forage on different location of more experienced individuals when productivity is low. By analysing foraging distributions of King Penguins (*Aptenodytes patagonicus*), Péron (2012) emphasised the impact of increases on sea surface temperatures. In her study, increases in temperature acted as one of the main drivers of foraging distribution on the species, inducing birds to search for resources in higher latitudes. It is not unreasonable to extrapolate that a similar scenario occurred in Cory's shearwater, since sea surface temperature (SST) was considered one of the most influential environmental predictors affecting the spatial distribution of both male/female and experienced/inexperienced individuals.

Finally, results from the stable isotope analysis depicted significant differences on the foraging ecology of female and male individuals. Results from the Carbon isotope analysis indicates that males foraged closer to land during chick provisioning seasons, while females tended to forage in more pelagic areas. These results support the conclusions made based on tracking and activity patterns, and fall into accord with data from isotopic analyses reported for the breeding season by Haug (2015) and Missagia (2015).

### 4.2 Environmental factors driving inter-sexual foraging segregation

Our study has considered the NAO as a surrogate of marine productivity. Studies by Osborn 2011; Paiva et al. 2013a, have unveiled details about the relationship between large scale atmospheric phenomena, driven by the NAO, and its effects on different levels of the food web. Negative values for 2010, 2011 and 2013 have coincided with significant increases in SST and reductions in CHLA, contrasting to what happens in 2012 and 2014, when positive NAO where observed. Despite the fact that the at-sea patterns were generally similar between sexes, sexual segregation was observed in years of greater environmental stochasticity, when marine productivity was the lowest. Birds travelled greater distances from their colony as well as spent more time in foraging areas when compared to years of higher productivity. Therefore, previous studies finding no evidence of sexual segregation in foraging behaviour and foraging strategies of Cory's shearwater (Ramos et al. 2009, Navarro et al. 2009) are partly explained by the fact that they were conducted solely during the incubation period, and presumably during years of relatively good environmental conditions. In fact, Ramos et al. (2009) suggested that subtler differences between the two sexes might exist, for instance in diving behaviour, or be detected in resource partitioning such as differences in the size of prey consumed between both sexes. While we did not examine such factors in this study, we were able to show significant differences between males and females in foraging distribution and oceanographic features within the birds' foraging areas, as well as in several aspects of trophic ecology. Foraging trip characteristics, habitat of foraging areas, trophic ecology (measured by stable isotope signatures) and body condition of females during years of poor environmental conditions were significantly affected, and thus differed from those of males (also from females during good years). Therefore, our study suggests that sexual differences in foraging ecology for the Cory's shearwater are likely to be relevant during poor environmental conditions. Our results make sense in the light of the competitive exclusion by the dominant sex, i.e. males over females (Phillips et al. 2004), which will occur mostly when environmental conditions are poor and resources are scarce. Furthermore, previous studies regarding such effects were conducted merely during a single breeding season, and thus failed to detect such important influence of environmental conditions on sexual foraging segregation.

Sex-specific niche divergence and habitat segregation can arise from a difference between sexes in parental roles (Thaxter et al. 2009) but the roles of male and female Cory's Shearwater do not appear to differ during chick-rearing (Navarro et al. 2009). However, males and females could forage in different areas in order to ensure that their chicks receive the optimum blend of prey species. Sex-specific differences were observed by analysing the first passage time (FPT; a proxy of foraging effort), where experienced females appear to spend less time searching for prey comparatively with inexperienced female. The foraging ecology of a marine predator is highly dependent on the abundance and distribution of prey (Bell 1991), and their dispersion is associated to large-scale ocean productivity (Hyrenbach et al. 2002). Thus the differences presented in foraging behaviour may be given by the contrasting productivity in the proximity of the island of Berlenga. The comparison of the two NAO values (2010; -4.64 and 2011; -1.6) suggests a large difference in oceanographic conditions (Osborn 2011), and therefore, may be a threshold in the surroundings of BER when the structure and functioning of marine ecosystems is severely affected (Walther et al. 2002) to force birds to leave their habitually productive grounds in search of higher prey availability.

### 4.3 Differential effects of the foraging choices on the trophic ecology of both sexes

Overall, the carbon isotopic signatures suggest that males seem to feed on prey inhabiting coastal environments (i.e. higher carbon signature) when compared to females, which exhibited a more exploratory and pelagic-oriented foraging pattern

(Quillfeldt et al. 2005). The option to forage over more pelagic environments, where prey availability is naturally more unpredictable (Weimerskirch 2007), might have impacted the body condition of females during our study period. Females seem to have been preying on low trophic level prey when compared to males, because they presented a lower nitrogen signature mostly during 2010, 2011 and 2013. There might be at least two reasons for this, 1) females were more explorative in 2010, 2011 and 2013 (i.e. years of poor environmental conditions, thus probably with lower food availability) preying on low trophic level prey, such as cephalopod or less nitrogen rich small pelagic fish species (e.g. *Scomber sp*; Paiva et al. 2010c), or 2) in years of food scarcity birds tend to attend more to fishery discards (Bicknell et al. 2013) and when doing so, males might gain access to higher trophic level prey in competition with females (Navarro et al. 2010). Although both hypotheses can be true, only the collection of more tracking and blood data along with vessel monitoring system data during subsequent years will disentangle the major driver of this pattern between females and males. Nevertheless, both groups were isotopically segregated even in years where both sexes were foraging on similar regions (i.e. a higher foraging area overlap in 2012 and 2014 than on the other study years), which certainly results from individuals feeding on isotopically different prey (Votier et al. 2011)

## 4.4 Conservation considerations

Much has been discussed concerning the impact of climate change on the distribution of seabirds. The general agreement points towards the prejudicial effects and fluctuations of highly influential environmental predictors, like sea surface temperature, dissolved oxygen and productivity rates (Schreiber and Burger, 2001, Irons et al., 2008). In fact, in years of food scarcity birds tend to attend more to fishery discards (Bicknell et al. 2013) which arises great concerns, given the danger that these behaviours represent to the birds (i.e. mortality through bycatch events; Barcelona et al. 2010). It is expected that changes in the environment should cause an increase on the global spatial distribution of Cory's Shearwaters, with experienced and inexperienced birds foraging in areas that until now have been ignored. Temperature increase can act as one of the main drivers of foraging distribution on the species, maybe inducing birds to search for resources in increasingly offshore areas and higher latitudes. Although previous studies have shown that Cory's Shearwater present a remarkable foraging plasticity, and may be among the species of seabirds better adapted to endure climatic variations (Dias et al. 2010; Paiva et al. 2010a), some concerns arise with these shifts in environment conditions. For instance, we can also speculate that experienced birds would be more affected by shifts in distribution than inexperienced ones, since these birds already engage in migratory events that takes them to more pelagic areas (Missagia et al. 2015).

## 4.5 Conclusion

This study documented a clear spatial segregation of female *versus* male Cory's Shearwaters as well as inexperienced *versus* experienced breeders, which increased during the last couple of years. Males relied heavily on static variables like the bathymetry of the area, while females were much more explorative, having a different combination and weighting of important variables (i.e. productivity proxies). Females undertook much larger foraging journeys than males, in years of greater stochasticity, similar to those during the pre-laying period. This study also adds to previous studies (e.g. Ramos et al. 2009; Navarro et al. 2009), proving that by analysing multiple year breeding seasons, sexual segregation in foraging behaviour and foraging strategies in Cory's Shearwater can be observed and thus, subtler differences between both sexes may be especially important in years of poor environmental conditions.

Our results also allow us to conclude that experience plays an important role determining the occurrence of spatial segregation in the species, showing it as a trait that should not be considered by itself, but added to a much bigger group of influencing factors. Climate stochasticity might have a significant influence on the spatial distribution of the species, exercising greater influence on male and experienced individuals (i.e. the group showing a more static distribution). Nevertheless, the true effects of such large-scale events cannot be encompassed on such a short-term study, making the continuity of monitoring the foraging ecology of this species crucial to understand the impact of climate change on this and other marine taxa.

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