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**CHICK PROVISIONING REGULATION IN CORY'S SHEARWATERS  
(*Calonectris borealis*):  
IS THERE A COORDINATION BETWEEN THE PAIR?**

Dissertação de Mestrado em Ecologia,  
orientada pelo Professor Doutor Jaime Albino Ramos e pelo Doutor Vítor Hugo Paiva,  
apresentada ao Departamento Ciências da Vida da Universidade de Coimbra

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**Chick provisioning regulation in Cory's Shearwaters  
(*Calonectris borealis*):  
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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 Paiva (Universidade de Coimbra).

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## Abstract

Procellariiform chicks are known to accumulate large amounts of lipid reserves during the nestling period. This characteristic was the subject of several studies during the last decades and instigated different theories about the presence of such reserves questioning a lack of coordination and regulation of feeding by parents. Though the few existing studies were inconclusive due in part, to the lack of suitable technology to test empirically those theories. We used as models of our empirical tests breeding pairs of Cory's Shearwaters (*Calonectris borealis*) from Corvo (oceanic colony) and Berlenga (neritic colony) Islands, locations with contrasting oceanographic characteristics in their surroundings. We deployed GPS-loggers on both parents of each pair of Cory's Shearwater during the chick-rearing periods of 2010 and 2015. We studied the at-sea behaviour and habitat use of the pairs tracked and we paid especial attention to the at-sea and at-colony encounters between each pair. To complement the study of the *C. borealis* pairs we also considered the isotopic niche (stable isotopic values of plasma) of each pair. Simultaneously, we monitored the feeding frequency, meal size and growth of each chick from the tracked pairs. We found that the behaviour of Cory's Shearwaters' pairs was strongly influenced by the breeding colony since pairs from Berlenga seem to better regulate chick provisioning when compared to birds from Corvo. In general, the pairs from Berlenga showed a higher frequency of at-sea encounters, used mostly the same high productive, cold water habitats in the surroundings of their breeding colony, exhibiting a rather small isotopic niche. They also met more often at the colony, translating in a better regulation of chick provision, with higher feeding frequency, moderate meal sizes and more regular daily mean mass increments. This pattern was broadly inverted for couples from

Corvo, where there was a higher frequency of long trips, with less encounters either at-sea or at-colony, broader isotopic niche, lower feeding frequency, bigger (though less frequent) meal sizes and a lower chick-growth. The visits to the colony at night to feed the chick seem to be directly related with proportion of encounters at sea between the parents. Overall, in the neritic colony where birds mostly perform daily short trips, the couple seem to better evaluate the nutritional requirements of the chick and adjust the feeding frequency according to the chick needs, which is more difficult to happen on the oceanic colony of Corvo.

**Keywords:** *Calonectris borealis*, Chick provisioning, Foraging, GPS tracking, Parental behaviour,

## Resumo

As crias de procelariformes são conhecidas por acumularem grandes quantidades de lípidos durante os primeiros dias de vida. Esta característica foi alvo de vários estudos nas últimas décadas e originou diferentes teorias acerca da presença destas reservas questionando a falta de coordenação e regulação da alimentação por parte dos progenitores. Os poucos estudos existentes são inconclusivos devido, em parte, à falta de tecnologia adequada para testar empiricamente essas teorias. Usámos como modelos dos nossos testes empíricos casais reprodutores de Cagarras (*Calonectris borealis*) das ilhas do Corvo (colónia oceânica) e Berlenga (colónia nerítica), locais com características oceanográficas contrastantes ao seu redor. Colocámos GPS-loggers em ambos os elementos de cada casal de Cagarras durante o período de desenvolvimento das crias de 2010 e 2015. Estudou-se o comportamento no mar e uso de habitat dos casais seguidos e prestámos especial atenção aos encontros no mar e na colónia entre os elementos de cada casal. Para complementar o estudo dos casais de *C. borealis* também tivemos em consideração o nicho isotópico (valores de isótopos estáveis do plasma) de cada casal. Simultaneamente, monitorizámos a frequência de alimentação, tamanho da refeição e crescimento de cada cria dos casais seguidos. Descobrimos que o comportamento dos casais de Cagarras foi fortemente influenciado pela colónia de reprodução uma vez que os casais das Berlengas aparentam uma melhor regulação do alimento da cria quando comparados com as aves do Corvo. Regra geral, os casais das Berlengas mostraram uma maior frequência de encontros no mar, utilizaram em grande parte os mesmos habitats produtivos e de águas frias, na vizinhança da colónia reprodutora, exibindo assim um pequeno nicho isotópico. Também se encontraram mais vezes na colónia,

traduzindo-se numa melhor regulação da alimentação da cria, com uma frequência de alimentação mais elevada, tamanhos de refeição moderados e incremento médio diário de massa mais regular. Este padrão inverte-se para os casais do Corvo, onde houve uma maior frequência de viagens longas, com menos encontros tanto no mar como na colónia, um nicho isotópico mais amplo, menor frequência de alimentação, maiores (embora menos frequentes) refeições e menor crescimento das crias. No geral, na colónia nerítica onde as aves executam principalmente viagens curtas diárias, o casal pode avaliar melhor as necessidades nutricionais da cria e ajustar a frequência de alimentação de acordo com as necessidades desta, algo que é mais difícil de acontecer na colónia oceânica do Corvo.

**Palavras-chave:** Alimentação de crias, *Calonectris borealis*, Comportamento parental, Forrageamento, Seguimento por GPS

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## Chapter 1 – Introduction



*"Caldeirão" – Corvo Island*

"The great book, always open and which we should make an effort to read, is that of Nature".

*Antoni Gaudi*



## 1.1 Growth characteristics of procellariiform seabird chicks

In order to live and feed at sea pelagic seabirds present several physical and behavioural adaptations. They are K strategists, which means that they have an extreme reproductive strategy: lay only one egg without a possibility of replacement in case of failure during incubation, invest significantly on parental care and have a long life span (Warham 1990, Onley and Scofield 2007). The single offspring of the Procellariiform seabirds facilitates the study of chick provisioning but the long chick-rearing period makes it more difficult to get detailed data on chick growth for the entire chick provisioning period (Bolton 1995a; Ramos et al. 2003). The foraging and chick food delivery of seabirds can be measured through their chick provisioning rate (feeding frequency and meal size), i.e. the net energy delivered during a given period, which will affect chick growth rate and survival, and parental fitness. Two main aspects should affect patterns of chick food provisioning: the limits of the chick's capacity when there are plenty of food available, and the adult persistence in searching for food when it is scarce.

The most important changes in meal mass given to seabird chicks occur in the mid-chick-rearing period and the chick provisioning rates drop before chicks reach their peak mass. For instance, in large Shearwaters such as the Cory's Shearwater *Calonectris borealis*, the energetic requirements of chicks may increase up to the age of 50 days (e.g. about half of the chick development period) and the average amount of food delivered increases up to the age of 30 days and stabilizes between 40 and 60 days (Ramos et al. 2003). Adult Cory's Shearwaters commonly feed their chicks large meals resulting in doubling their mass overnight,

and about 60% of their intake food is converted into biomass (Hamer and Hill 1993).

Procellariiform seabirds are known to accumulate large amounts of lipids reserves during the nestling period (Knonarzewski and Taylor 1989, Warham 1990). Their body mass before fledgling is composed by up to 60% of lipids (Ricklefs, White and Cullen 1980) and the chicks may weight 150% of the parent's body mass. The explanation of nestling obesity in pelagic seabirds has stimulated many ecological evolutionary studies: 1) Lack (1968) firstly mentioned that fat accumulation would be an insurance against temporary periods of food shortage; 2) Ricklefs and Schew (1994) refined the Lack hypothesis and argued that nestling obesity evolved as a response to "chronic cumulative effects of stochastic variation in foraging success and food delivery by individual parents"; 3) Hamer and Hill (1993), Bolton (1995a;1995b), and Hamer et al. (1997) examined natural variation in feeding frequency and meal size to evaluate whether this was related with the chick requirements or with temporal variations in food availability; 4) Lorentsen (1996) and Granadeiro et al. (1998) monitored chick food provisioning in relation to adult body condition. The main conclusions of these studies is that parents may be able to adjust chick provisioning in relation to the requirements of their chicks if there is no food shortage (Bolton 1995a), however, parental body condition should be a key factor in explaining patterns of chick food provisioning (Lorentsen 1996).

Life history theory clearly predicts that body condition of K-strategist parents determines the cost they can afford for the current reproductive attempt considering its possibilities for future survival and reproduction during their long life span (Stearns 1992). It is well known that patterns of chick provisioning may change both within and between years caused by the seasonal and annual

variation in food availability. In studies with chicks from Black-browed Albatross *Diomedea melanophris*, Grey-headed Albatross *Diomedea chrysostoma* (Huin et al. 2000) and with White-tailed Tropicbirds *Phaethon lepturus* (Ramos and Pacheco 2003) chicks that failed to fledge received smaller meals and had a low frequency of feeding than the successful chicks. The differences in provisioning rate affected chick growth rates, peak and fledging mass of these three species. However, other studies found no relationship between parental foraging strategies and chick condition, since the meal sizes were not related with the trip duration, meal mass and chick condition (Hamer and Hill 1993). In an experiment with Cory's Shearwater where one group was deprived of 30g of food the adults with the deprived chick increased the frequency of feeding events but did not increase the size of feeds (Granadeiro et al. 2000). The growth rate of the food deprived chicks was similar to that of control chicks, which provides evidence of a change in behaviour of the pair that may lead to some kind of coordination.

In conclusion both stochastic (related with characteristics of breeders) and environmental (related with variation in food availability) factors are likely to be important in explaining chick provisioning patterns. When environmental conditions are very poor, it is clear that environmental stochasticity plays the major role in explaining chick provisioning, particularly in tropical areas, where acute food shortages are more common (Ramos et al. 2002, Catry et al. 2013). Nevertheless, the possibility that adults can adjust chick provisioning in relation to the requirements of their chick (Bolton 1995a) mean that some sort of coordination and/or cooperation might exist in order to evaluate properly the nutritional status of their chick.

Seabirds are known for their long-term pair bonds that can last for a lifetime (Black 1996). Losing a mate leads to an amount of energy spent to find a new mate, and may result in a missed breeding season. Therefore, coordinated parents tend to have higher breeding success (Bried and Jouventin 2002). Because biparental care is needed during the incubation and chick-rearing periods, coordination among the pair is expected in several aspects such as foraging trips to the sea, and the time spent in the colony defending the nest and incubating the egg. Before the development of devices such as GPS-loggers, it was very difficult to know if the pair maintained contact during the migration, but present studies with Scopoli's Shearwater (*Calonectris diomedea*) showed that the two members of the breeding pair do not migrate together but spend almost the same time traveling and in the similar nonbreeding areas. Another curious fact is that individuals that nest close to each other tend to travel for nonbreeding areas closer to its neighbours (Mülller et al. 2015). This is typical of Shearwaters, which have high natal philopatry and present high nest site fidelity (Rabouam et al. 1998), which again suggests some kind of coordination between the breeding pair.

## **1.2 Coordination between the pair in feeding their chick**

Seabirds are able to adjust chick provisioning by changing the time spent on foraging, the volume of food delivered to the chick or both (Weimerskirch et al. 2000). Chicks may not accept all the food when visited by both adults on the same night and they may influence the provisioning behaviour of the parents by changing the begging intensity or frequency (Granadeiro et al. 1998). Parents from many

avian species are able to perceive the nutritional status of the chick by the offspring solicitation behaviour, and apparently can adjust their provisioning accordingly. This ability of interpretation of the begging behaviour to provide information on the nutritional status of the chicks has been recognized also in some seabird species (Henderson 1975; Harris 1983). Procellariiform chick growth characteristics make coordination among the pair important to successfully raise the chick. Such coordination is particularly relevant because parents leave the chick alone and venture in long foraging trips at sea. If adults overfed their chick in order to avoid the possibility of undernourishment, this might be related with the lack of coordination and regulation of feeding by both parents.

The adults normally feed their chick at intervals of several days. The feeding events may occur independently of their partner or the parents may coordinate themselves. In the first case the nutritional status of the chick at the end of one feed event may not provide reliable information regarding its requirements for the next feed. When parents coordinate themselves they should perceive the status of their chick and regulate food provisioning accordingly. Coordination between the pair for chick food provisioning may arise in evolutionary terms because if the average level of provisioning were simply that required to fulfil the daily chick maintenance and growth requirements many chicks would be periodically underfed given stochastic variation in the foraging success of individual parents (Ricklefs 1990; Granadeiro et al. 1998). However, several studies support the fact that lipid accumulation is related to stochastic variation in food resulting from a lack of feeding regulation because each parent fed the chick independently of the chick nutrition level, and the adults delivered consistent amounts of food to the chick. (Hamer et al. 1998) used supplementary feeding in Manx Shearwater (*Puffinus*

*puffinus*) to test if parents were able to adjust the chick provisioning accordingly to the nutritional level of the chick and found no difference between the control and the experimental group before the supplementary feeding test began, but after, chicks from the experimental group received fewer feeds from their parents. However, the mass of food delivered was similar between both groups. Presumably, nestling obesity may in some cases play an important role to prevent chick starvation from the stochastic variation in food provisioning, and when environmental conditions are favourable lipid accumulation may not be related with a lack of coordination between the parents (Hamer 1994).

Cory's Shearwaters and many pelagic seabird species present a dual foraging strategy when food resources are scarce. This behaviour represents a mechanism to adjust the demands of the chick with the maintenance of their own body condition. A dual-foraging strategy may be particularly relevant when birds face low food availability near the colony (Granadeiro et al 1998). Parents that use a dual-foraging strategy do not co-ordinate their foraging in order to prevent the chicks without being fed (Magalhães et al. 2008), so the chicks from parents with that strategy have longer intervals between feeds than the chicks from colonies where this foraging strategy is reduced. In some situations, the adults increase the frequency of visits to the nest, showing evidences that they are able to modify their behaviour in response to short-term chick requirements (Granadeiro et al. 2000). Studies with Cory's Shearwater have shown that chick feeding rate was not entirely adjusted to their body mass, but was dependent from the interval since the last meal (Hamer and Hill 1993), suggesting an intrinsic rhythm that may control chick food provisioning instead of a regulation by the pair. However, Cory's Shearwaters may respond to short-term variation in the nutritional status of their offspring and



adjust their provisioning rate accordingly as shown experimentally by Granadeiro et al. (2000): one group of chicks was deprived of food and other group was given a food supplement; this last group of chicks reduced their begging behaviour once their body condition increased. In opposition the group of chicks deprived of food were only capable to sustain their condition before the beginning of the experiment, and thereafter maintained high levels of begging. This suggests that the behaviour of the chicks should have a strong influence in the provisioning by the parents.

### **1.3 Regulation of chick food provisioning and the marine environment**

The procellariiformes typically visit the colony infrequently, which may occur because they forage over a vast oceanic area, and the food resources are scarce and unpredictable (Weimerskirch 2007). Thus the fat accumulation of the chicks may exceed the amount needed to withstand fasting periods. However, the persistent unfavourable oceanographic conditions resulting in prolonged periods without parental visits to the nest are infrequent. For some species, the foraging trip duration will depend on the condition of the birds at the end of their previous trip (Weimerskirch et al. 1994; Granadeiro et al. 2000). Moreover, the chicks will remain unfed for longer periods if both parents perform long trips at the same time, thus co-ordination among the pair may be crucial to maintain the nutritional status of the chick. Congdon et al. (2005) suggested that Wedge-tailed Shearwater *Puffinus pacificus* perform short-trip cycles on the same day, or the day before, when their mate returns from a long foraging trip; therefore, the return from the mate that performed a long-trip cause the changeover by interaction with its partner

probably at sea or at the nesting colony. Weimerskirch et al. (2001) showed, for the Yellow-nosed Albatross (*Thalassarche chlororhynchos*), that the adults are able to regulate chick food provisioning when feeding conditions are better.

During the breeding season, seabirds face conflicting decisions in order to visit their nests regularly to incubate the eggs and feed the chicks, because they have to maintain their body condition in levels that do not compromise their future breeding attempts (Stearns 1992). The maintenance of adult body condition depends, to a great extent, on the foraging conditions around the breeding colonies, which may be conditioned by changes in oceanographic conditions that will influence the foraging strategies of the birds (Ramos et al. 2002, Ramos et al. 2015). To study the significance of parental body condition in chick provisioning we should evaluate meal size, feeding frequency and chick growth. For instance, in the Antarctic Petrel *Thalassoica Antarctica* Lorentsen (1996, 2005) found that: a) there was a high correlation between the average meal size and the growth rate of the chick, b) the body condition of the adult at the time of hatching was correlated with the average size of meals delivered, c) by day 30 the body mass of the chick is influenced by the pair body condition at the first incubation shift and at hatching, and d) by day 30 the chicks from parents with good body condition had a body mass twice the expected compared with those chicks whose parents had poorer body condition, suggesting that the amount of effort spent during the chick-rearing is regulated by the body condition of the adults (Lorentsen 1996).

Seabirds are known to form strong social bonds and one interesting aspect of their at-sea behaviour is the occurrence of large rafts (Weimerskirch et al. 2010), where the use of social information may occur with many purposes like coordination of the foraging and nest attendance. If seabird mates can take

advantage of this exchange of social information in conjunction with their own personal information and experience, it is expected that they will be able to coordinate better their effort to take care of their young. Recent studies concerning the at-sea behaviour of seabird mates indicate that at sea socialization might be an opportunity for the pair to coordinate their colony attendance (Weimerskirck et al. 2010; Hamer et al. 2002). Moreover, many studies suggest that mates show more similitude in their at-sea behaviour when compared to random birds of the same population (Müller et al. 2015).

A possible coordination between the adults may be connected with the different marine environments that influence their behaviour. So, to investigate this we need to study breeding pairs from colonies with different oceanographic characteristics. In this study we deployed GPS-Loggers on both parents of one neritic (Berlenga Island) and one oceanic (Corvo Island, Azores) colony. The oceanographic conditions in the colony of Berlenga are distinct from those of the Corvo colony, in that the first is neritic and the second is oceanic, and central place foragers like the Cory's shearwater have to adapt their foraging accordingly. Productivity is high near Berlenga, because it is situated in the continental shelf surrounded by shallow waters and rich foraging grounds where coastal upwelling events are common (Sousa et al. 2008; Ceia et al. 2014), so the birds from this colony present a lower foraging effort due to the abundance of food resources influenced by the Canary Current plus the bathymetric characteristics and continuous upwelling along the Portuguese coast (Paiva et al. 2013). On the other hand, oceanic colonies in the Azores archipelago such as Corvo are surrounded by less rich marine environments. Both populations make short and long trips, in order to search for resources to feed their chicks or to feed themselves and

maintain their body condition. However, Paiva et al. (2010) showed that birds from oceanic colonies make longer trips and spent more time travelling to distant areas than birds from neritic areas. During short trips birds use mostly shallower waters close to the colony, and during long trips birds search for areas with high chlorophyll *a* concentration and low sea-surface temperature. In the oceanic colony birds are particularly known to forage above the seamounts, frontal regions and other oceanographic structures that enhance marine productivity (Morato et al. 2008a; 2008b).

To analyse the possible existence of coordination between the pair in foraging and feeding its offspring, it is expected that in the neritic colony (Berlenga) birds show high levels of coordination since they perform shorter trips and therefore move more regularly between sea and colony, where they can meet more often and assess the nutritional status of the offspring. In the oceanic colony a dual-foraging strategy should be dominant and the at-sea encounters between the pair will be less frequent, which should provide lower levels of coordination. Using the repeatability index comparing the mates' behaviour with other individuals randomly paired will provide information related with the pair coordination showing the parameters where the members of the pair have more similitude. In addition, the isotopic niche using plasma of each pair will provide information that may support the hypothesis that the coordination will be higher in the neritic colony; it is expected that the isotopic niche will be similar between each member of the pair in the neritic colony, since they forage in the same areas, whereas the members of the pairs from the oceanic colony are more likely to feed in different areas. To see the influence of the behaviour of the adults in their chicks we monitored the feeding frequency, meal size and chick growth. We expected that chicks from pairs with

higher levels of coordination will be fed more frequently. Also, the presumed lower level of coordination in the oceanic colony may lead to a higher meal size to prevent the chick from starvation.



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## Chapter 2 – Methods



*Corvo Island*





## 2.1 Study species

Cory's Shearwater (*Calonectris borealis*) evaluated as Least Concern according to the IUCN Red List of Threatened Species, is a midsize procellariiform seabird species that breeds mostly in the Atlantic islands of Berlengas, Azores, Madeira and Canaries (Paiva et al. 2010). The Azores have about 188 000 breeding pairs, 3735 to 10 524 pairs (2012) only in Corvo Island (Oppel et al. 2014) and about 1000 in Berlenga (Lecoq et al. 2011). Cory's shearwaters are long-distance migrants and during the non-breeding season, between December and February, they migrate mostly to the South Atlantic productive areas (Ramos et al. 2012) and during winter they can be found in Brazil, South Africa and Southern Central Atlantic (Ramos et al. 2009). The breeding season occurs between April and November. Nests are placed in natural cavities in rocks but they also can reuse burrows from other animals or dig their own burrow, which can reach more than two meters deep. Also, due to conservation measures they have been using some artificial nests (Figure 1B). Before laying the egg, females take a long trip (around twenty days) to build up body reserves and then they lay their single egg in late May/early June and during the incubation period, which may last around 54 days, the pair exchange shifts to take care of the egg and defend the nest. The chick-rearing lasts from late July to early November and during this stage parents alternate foraging trips to feed the chick and also to maintain their own body condition. This species presents a central place foraging strategy and feeds on pelagic fish (sardines, horse mackerel and garfish) and cephalopods (Xavier et al. 2011), makes long trips at sea in search of food and feeds the chicks at night. The chicks grow at a lower rate by the end of September, reduce their body size and

their wings grow until early November when fledge and thus leave the nest at night, on the first incursions to the open ocean (Warham 1990).



**Figure 1.** Cory's Shearwater *Calonectris borealis*. A – Adult in the nest with their chick.  
B – Chick

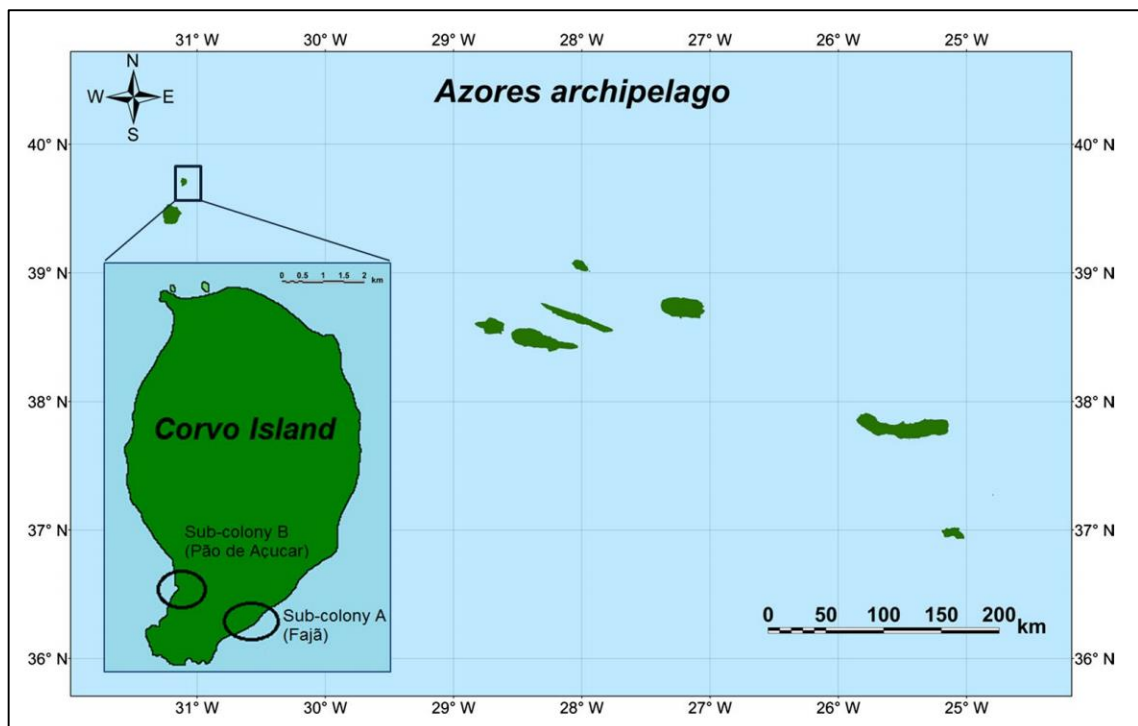
## 2.2 Study area

This study was made in two distinct areas of the Atlantic Ocean, Corvo Island (39° 40' 19" N 31° 06' 42" W) in the Azores archipelago and Berlenga Grande (39° 24' 52" N 9° 30' 22" W) in the Berlenga archipelago.

### 2.2.1 Corvo Island

Corvo Island (Figure 2) is the smallest of the nine islands of the Azores archipelago with 17.13 km<sup>2</sup>, 6.4 km long by 4 km wide and a resident population of about 400 habitants. Belongs to the western group and is on the North American tectonic plate to the west of the Mid-Atlantic Ridge. In the past a large numbers of seabirds nested in the Azores but the human settlement, and consequently of invasive species such as the Black Rat (*Rattus rattus*), the Brown Rat (*Rattus norvegicus*), the House Mouse (*Mus musculus*), Domestic Cats (*Felis catus*) and

other land mammals reduced the populations of seabirds, and the number of species and individuals occupying these islands decreased dramatically. The largest and most abundant seabird species on the island is the Cory's Shearwater but other species can be found like the Manx Shearwater, the Little Shearwater (*Puffinus assimilis*), the Common Tern (*Sterna hirundo*) and the Roseate Tern (*Sterna dougallii*).



**Figure 2.** Corvo Island, Azores, Portugal (39°40'N, 31°06'W) showing the two studied sub-colonies (after Ceia et al. 2014).

### 2.2.2 Berlenga archipelago

The Berlenga archipelago (Figure 3) is located in the Atlantic Ocean about 5.5 nautical miles off the Portuguese coast (about 10 km off the coast of Peniche) and in addition to Berlenga Grande (the largest island with 0.788 km<sup>2</sup> and about 1.5 km long by 0.8 km wide) also includes two other granitic islands, Farilhões and Estelas. Natural Reserve since 1981, this archipelago is of extreme importance for

our study species *Calonectris borealis* where there are about 1000 breeding pairs (Lecoq et al. 2011).

These islands are still nesting site of other important seabird species, such as the Madeiran Storm-Petrel (*Oceanodroma castro*) or the European Shag (*Phalacrocorax aristotelis*). The Yellow-legged Gull (*Larus michahellis*) population breeding in the island is very large with an estimate population of 13150 individuals in 2013 (Morais et al. 2013). The Common Murre (*Uria aalge*) is the most emblematic seabird of the archipelago and in the past bred in large numbers, about 6000 breeding pairs in 1939 (Lockley 1952) but their population has decreased dramatically in the recent decades with the last individual observed in 2012 (Lecoq et al. 2012). The terrestrial fauna comprises several birds like the Pallid Swift (*Apus pallidus*), the Peregrine Falcon (*Falco peregrinus*), the Common Kestrel (*Falco tinnunculus*) the Redstart (*Phoenicurus ochrurus*), small mammals like the Common Rabbit (*Oryctolagus cuniculus*), and the Black Rat both introduced by man and even small reptiles like the Berlenga's endemic Carbonell's Wall Lizard (*Podarcis carbonelli berlengensis*). Berlenga have a particular flora and some endemism like the Armenian-of-Berlenga (*Armeria berlengensis*) and the *Herniaria berlengiana* an endemic plant considered vulnerable. However, the most notorious is the Hottentot Fig (*Carpobrotus edulis*), exotic plant introduced on the island in the 50s as an ornamental plant and quickly spread throughout the island. In addition to the problem of competing with endemic plants, reduced the burrows available for the Cory's Shearwater nests. This problem led to conservation measures to restore the flora of the island and it is expected that within a few years all this plant is removed. There are some others threats to biodiversity of the island, particularly to seabirds. The Black Rat is known to prey on eggs of Cory's

Shearwater and that is why protection measures should be taken (Hervías et al. 2013). Fishing activities also cause the death of several species of seabirds every year, so it is important to study the places where these birds feed and preserve them.



Figure 3. Berlenga, Portugal (39°24'N, 9°30'W). [www.icnf.pt](http://www.icnf.pt)

Climatic factors can influence the breeding success of pelagic predators as a result of alteration in prey abundance (Genovart et al. 2013). Seabirds spend most of the time at sea and the trans-equatorial Atlantic migratory Cory's shearwater may face different weather conditions during breeding and non-breeding periods (Genovart et al. 2013), however is in the breeding season that birds are associated to highly productive areas throughout the year (Peron et al. 2010). Also, some large-scale seasonal climatic indices like the North Atlantic Oscillation (NAO) are related with climate change (Paiva et al. 2013). The NAO index is a north-south oscillation in atmospheric mass between the subtropical Atlantic and the Arctic trough the interaction between the high-pressure centre near Azores and the low-pressure centre near Iceland. The NAO values fluctuate every year and negative values are related with a decrease in the sea surface temperature (SST). This happens because of the strong winds that support the upwelling events and negative NAO years are characterized by an increase in marine organism from lower trophic levels to top predators like our study species.

## 2.3 Fieldwork

Fieldwork in Corvo Island took place in August 2015 and in Berlenga in September 2015, both during the chick-rearing period. To complement this study, we used data previously collected in the same colonies during the same period in 2010 (Ceia et al. 2014; 2015).

In Corvo Island nest selection was made in the colony of "Pão de Açúcar", where most of the nests had been identified in previous years. Nests which have breeding pairs with chicks and reasonably easy access were selected, since the chicks had to be removed from the nest twice a day every day during the two-week period. Eleven nests were selected, 9 housed in rock holes and 2 located in old typical barns, where 1 was on surveillance 24 hours a day using an infrared camera broadcasting live in the website <http://cagarro.spea.pt>.

In Berlenga 23 nests were selected under the same conditions referred above, breeding pairs with chick and easy access. The selection occurred in "Melreu" colony. The adults were captured and identified by the ring, weighed with the Pesola and measured (wing and tarsus) and the GPS logger devices were placed to be collected later during the last weighing of the chicks. Also in this phase were collected again the adults' biometrics (wing and tarsus) and weight.

Chicks were weighed using a Pesola (1 kg) every day starting at 09:00h in the morning and chicks were weighing always in the same order. The chicks were weighed again at 21:00h before being fed.

For the stable isotopes analysis (SIA), about 0.5 ml of blood was collected from the tarsal vein of each adult birds using a 1ml syringe. The collected blood was stored in Eppendorf tubes and kept cold in the field and centrifuged within

about 3-4 h to separate plasma from red blood cells (RBC). After this process both tissues were stored frozen at -20°C until processed for SIA.

## **2.4 GPS loggers: programming, deployment and specifications**

Both adults of each pair were equipped with GPS loggers. To program the GPS-loggers they were connected to a computer and using the @trip PC software the data was clean and after calibrated the device was programmed to collect data every 5 minutes. Battery saving settings were also set to extend the period of data collection. The GPS logger has a GPS receiver, an antenna, the data-logger, user interface circuits and a battery (designed accordingly with Steiner et al. 2000) and weight 15g. In order to reduce weight and dimensions of the device the hard plastic case was removed and substituted by a thermos-retractable rubber 7 cm long sealed with heat. This rubber sleeve also makes the device waterproof. This device has to be retrieved in order to access the data.

To hold the devices in the birds were used small pieces of a specific Tesa tape (Wilson et al. 1997) that were glued to the back feathers allowing the birds to move freely. The procedure (illustrated in Figure 4) was performed rapidly without exceeding 10 minutes in order to reduce the stress in the bird.

In Corvo Island were tracked 19 pairs in August 2010 and 4 pairs in August 2015 (Table I). In Berlenga were tracked 4 pairs in August 2010 and 5 pairs in September 2015. More GPS-loggers were deployed in others nests but the birds did not come back to the nest when we were in the Island, so we were not able to collect data on both members of the pair.



In addition to the geographic coordinates, date and time, these devices also record information on altitude, speed and distance to the colony.



**Figure 4.** GPS-Logger deployment

**Table I.** Total number of GPS-Loggers used during fieldwork in Corvo and Berlenga during the two years (2010 and 2015)

<b>Year</b>	<b>Colony</b>	<b>Loggers deployed</b>	<b>Not recovered</b>	<b>Females tracked</b>	<b>Males tracked</b>	<b>Mates tracked</b>
<b>2010</b>	<b>Berlenga</b>	34	5	16	13	<b>4</b>
	<b>Corvo</b>	45	1	20	24	<b>19</b>
<b>2015</b>	<b>Berlenga</b>	20	2	7	11	<b>5</b>
	<b>Corvo</b>	15	5	6	4	<b>4</b>

## 2.5 Stable Isotope Analysis (SIA)

Stable Isotope Analysis (SIA) was conducted to describe the foraging ecology and prey selection by the  $\delta^{15}\text{N}$  ratio. In addition, the  $\delta^{13}\text{C}$  analysis gives us the spatial distribution. Near the coast the  $\delta^{13}\text{C}$  values are higher and decrease as it moves offshore, because coastal areas are richer in organic matter.

Plasma has a turnover rate of about 7 days and reflects the trophic choices made in the last trips before sampling, around 7 days (Cherel et al. 2005a; Inger &

Bearhop 2008). On the other hand, RBCs are regenerated every 12-22 days, reflecting the trophic ecology of the last few weeks.

For this particular study, the isotopic values from the pair are more important than the individual values once they will give information not only about the feeding habits of the individuals but from the pair. This kind of information is crucial to evaluate the existence of coordination of the pair since we expect that in the neritic colony where the resources are more predictable and abundant the birds will forage in the same smaller area and consequently have a similar isotopic signature. On the other hand, birds from the oceanic colony are expected to have more distinct isotopic signatures due to the fact that they explore a larger area of ocean in their long trips and consequently will feed from different places.

Before the SIA analysis the plasma and RBC was subject to successive washings with a 2:1 solution chloroform/methanol for delipidation (Cherel et al. 2005b). About 0.35 mg of each sample of plasma and RBC were weighed inside tin cups in a microbalance with the help of tweezers that were sterilized with ethanol between each weighing to avoid contaminations.

## **2.6 Estimation of meal size, feeding frequency and chick growth**

(1) meal size was estimated by the difference between the weighing at 9h and the previous weighing at 21 h. This value does not take into account the mass lost by the chick through physiological processes like excretion and respiration between the two weighings. In order to have more precise values we used the equation  $-i(r1+r2)/2$ , where  $i$  is the interval between weighings, and  $r1$  and  $r2$  are

the rates of mass loss over the 4 h before and after a meal, respectively, according to Hastings & Peacock 1975; (2) feeding frequency was calculated as the proportion of nights the chick received food, from the overall amount of time both parents were simultaneously being tracked; (3) chick growth was computed as the mass increment per day (i.e. mean daily mass variation), determined with a linear regression of body mass on age. In order to estimate the age of the chicks from Corvo and Berlenga in 2010 and 2015 we used a curve from a study in Berlenga (Granadeiro 1991). The wing-length (mm) was used to determine the age in days. On Corvo, one nest was followed daily with a webcam, and the actual age was only 2 more days than the age determined based on the curve. This shows that the curve values were reliable.

## **2.7 Data analysis**

### **2.7.1 Trip filtering**

The GPS-Logger collects data from the bird's movements for several days, collecting data when the bird is moving and when is in the colony.

After the GPS data collected they were analysed to identify the individual trips, these being divided by taking into account the distance to the colony. For each bird were divided and identified every trip and were also divided in long trips and short trips using the date and time data collected by the device. It was assumed that individuals were in the colony when the distance to the colony was 0 or close and a new trip was initiated when the distance begin to increase. Sometimes when the bird is in the nest the device stops collecting data and starts again when the

bird is again away from the nest to start a new trip. All coordinates from the period of time inside the nest were removed leaving only the arrival and departure.

### **2.7.2 At-sea and at-colony encounters**

To examine if there were meetings at sea between the parents, the data collected by GPS-Loggers were imported to the ArcGIS software. The data from the two colonies were used (Corvo and Berlenga) and the two study years (2010 and 2015). To view spatially if there was interaction between the pair, for each day the coordinates of each member were checked and identified with different colours for the male and the female. When geofixes of male and female were at less than 0.5 km from each other we counted as possible encounter between the pair (at least some degree of socialization between pair members). This proximity was then scrutinized to see if the proximity of the coordinates occurred at the same time, because only in this case could be considered that the pair met at-sea. The data of coordinates that respected this premise were subsequently exported to form a new data matrix with the coordinates of all meetings at sea per pair and per colony for further analysis and comparison. This visual data analysis also allowed to perceive for each day their behaviour i.e distance to colony, time foraging, time they return to the colony and the ocean area used by the pair. At-colony encounters of the pair were also identified through the analysis of the GPS-loggers' data, as periods of at least 10 min in which the pair was joint at the colony. The proportion of time mates met at-sea and at-colony were defined as the number of encounters recorded per day from the overall amount of days the pair was being simultaneously tracked.

Kernel Utilization Distribution (Kernel UD) was estimated from the GPS coordinates collected in each pair using the *adehabitatHR* R package (Calenge 2006). The main foraging areas of the pair were represented by the 50% and 95% kernel UD contours. The North Atlantic Oscillation (NAO) values (<https://climatedataguide.ucar.edu/climate-data/hurrell-northatlantic-oscillation-nao-index-station-based>) were used as an environmental predictor for the study area (North Atlantic). To complement the environmental information, we used the chlorophyll *a* concentration (Chl *a*) and the sea surface temperature (SST), both downloaded from <http://oceanocolor.gsfc.nasa.gov>.

### **2.7.3 Statistical analysis**

General Linear Models (GLMs), followed by post-hoc multiple comparisons Bonferroni corrected tests, investigated the effect of the interaction between year (2010 vs 2015) and colony (Corvo vs Berlenga) on regional (Mean monthly NAO index) and local (e.g. chlorophyll *a* concentration) environmental predictors in the colony surroundings (100km around the breeding colony).

We used the (1) Intraclass Correlation Coefficient (ICC) or Repeatability (*r*) (Nakagawa and Schielzeth 2010) to ascertain which parameters had most similarity between the pair in contrast with the other individuals paired randomly. The foraging and trophic parameters for which the *P* value associated with the Repeatability were significant are listed in the table IV and for all the four main parameters group measured (1) Trip characteristics, (2) Spatial ecology, (3) Habitat foraging areas and (4) Trophic ecology we obtained significant values. Tests corrected for (1) year, (2) colony, (3) individual and (4) Nest (random factors).

Repeatability was computed using between-group variance and within-group variance components obtained from linear mixed models (LMM) using restricted maximum likelihood. To produce the appropriate variance components, we performed LMMs that included Sex as a fixed factor and Colony, Year, Individual and Nest as random factors. Although we were interested in the variance in the aforementioned four main parameter groups explained by the nest, we included the additional random factors to avoid inflating nest repeatability estimates that were due to variation attributable to year differences or to the similarity among observations from the same individuals.

Linear mixed models (LMMs) were also used to investigate the relationships between (A) mates foraging at-sea characteristics; (B) at-sea and at-colony behaviour of mates; (C) mates' behaviour and parameters of chicks' provisioning and growth.

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## Chapter 3 – Results



*Fort of São João Baptista das Berlengas*





### 3.1 Environmental variability

The mean monthly NAO index and the SST were significantly lower in 2010 when compared to 2015 (Tables II and III). SST on the surroundings of Corvo Island in 2015 was significantly higher than that of 2010 and in Berlenga during 2010 and 2015. Waters surrounding Berlengas were significantly more productive (higher Chl *a*) in 2015 than all other possible island-year combinations. SST anomalies were significantly higher in Berlengas during 2010 when compared to all other possible island-year combinations (Tables II and III).

**Table II.** Mean ( $\pm$ SD) regional and local environmental predictors in the surroundings of Corvo and Berlenga Islands between 2010 and 2015. wNAO – extended winter (December-March) north Atlantic Oscillation Index. Mean monthly NAO index and environmental predictors for the spring-summer (March-August) of each year.

Year	2010		2015	
Colony	Corvo	Berlenga	Corvo	Berlenga
<b>Regional environmental predictors</b>				
wNAO index #	-4.6		3.6	
Mean monthly NAO index	-1.9 $\pm$ 0.6		2.2 $\pm$ 1.0	
<b>Local env. predictors</b> (within 100 km of the colony)				
Chlorophyll <i>a</i> concentration (Chl <i>a</i> ; mg m <sup>-3</sup> )	0.8 $\pm$ 0.2	0.5 $\pm$ 0.1	0.3 $\pm$ 0.1	1.0 $\pm$ 0.4
Sea surface temperature (SST; °C)	16.4 $\pm$ 0.6	19.9 $\pm$ 0.5	20.8 $\pm$ 0.7	16.9 $\pm$ 0.9
Sea surface temperature anomaly	-0.9 $\pm$ 0.2	1.2 $\pm$ 0.5	1.0 $\pm$ 0.3	-0.8 $\pm$ 0.3

# (extracted from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based/>)

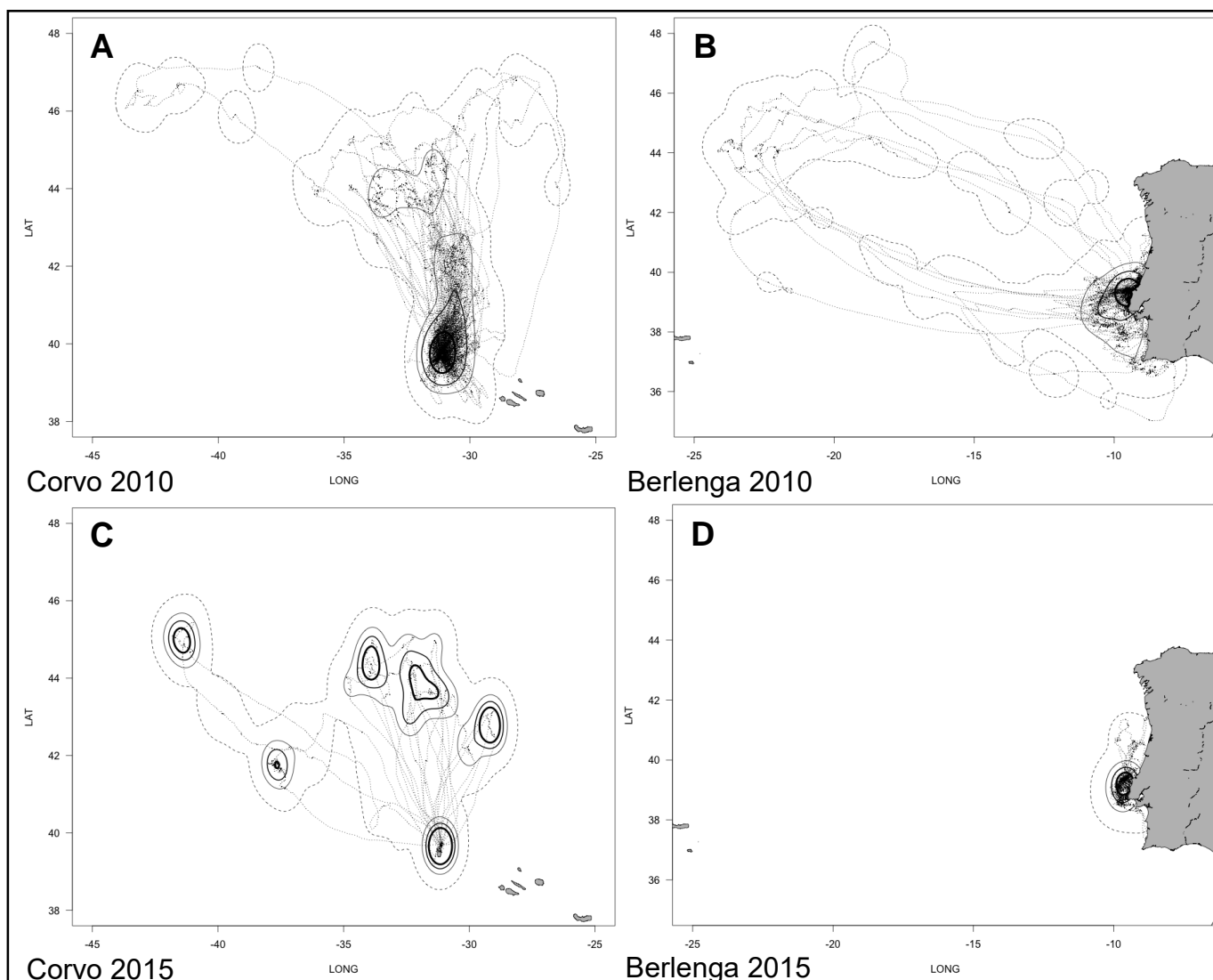
**Table III.** General Linear Models (GLMs) testing the effect of year (2010 vs 2015), colony (Corvo vs Berlenga) and their interaction on regional and local environmental predictors in the colony surroundings (100km around the breeding colony) as shown in Table II. wNAO – extended winter (December-March) north Atlantic Oscillation Index. Mean monthly NAO index and environmental predictors for the spring-summer (March-August) of each year. Significant results are shown in bold. Effect was evaluated with Post-hoc multiple comparisons with Bonferroni correction.

Variables	Year			Colony			Year * Colony		
	GLM	P	Effect	GLM	P	Effect	GLM	P	Effect
<b>Regional environmental predictors</b>									
wNAO index #	—	—	—	—	—	—	—	—	—
Mean monthly NAO index	$F_{4,10} = 25.6$	<b>&lt;0.001</b>	2010 < 2015	—	—	—	—	—	—
<b>Local environmental predictors (within 100 km of the colony)</b>									
Chlorophyll a concentration (Chl a; mg m <sup>-3</sup> )	$F_{9,148} = 1.50$	0.16	—	$F_{9,148} = 1.58$	0.13	—	$F_{9,148} = 1.90$	<b>0.05</b>	Berlenga 2015 > all others
Sea surface temperature (SST; °C)	$F_{9,148} = 2.59$	<b>0.01</b>	2010 < 2015	$F_{9,148} = 1.40$	0.19	—	$F_{9,148} = 2.62$	<b>0.01</b>	Corvo 2015 > all others
Sea surface temperature anomaly	$F_{9,148} = 1.43$	0.19	—	$F_{9,148} = 1.31$	0.23	—	$F_{9,148} = 2.30$	<b>0.02</b>	Berlenga 2010 > all others

# (extracted from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based/>)

### **3.2 Spatial ecology**

The spatial foraging distribution of birds from Corvo and Berlenga was very contrasting between 2010 and 2015. In 2010, a year of a very negative wNAO (-4.6), birds from Corvo mostly performed short trips foraging in the surroundings of their breeding colony, while birds from Berlenga performed a comparatively higher amount of long foraging excursions. In 2015, a year of a very positive wNAO (3.6), birds from Corvo invested more on long foraging trips, searching for food farther from their breeding colony, while birds from Berlenga performed only short trips, foraging closer to their breeding location (Figure 5).



**Figure 5.** Home range (Dotted lines) and foraging areas (solid lines) for the tracked Cory's shearwaters pairs during the chick-rearing seasons of 2010 and 2015 in Corvo and Berlenga.

When we analysed some parameters of trip characteristics, spatial ecology and habitat of foraging areas, we verified that some of these parameters were more similar between the members of the pair than when compared with random pairing. Namely, mates were more similar in their maximum distance to colony (km), 50% Kernel UD overlap, Area of the 50% Kernel UD, bathymetry (m), chlorophyll a

concentration ( $\text{mgm}^{-3}$ ) and carbon isotopic signature from plasma ( $\text{‰}$ ), when compared to random mates (Table IV).

**Table IV.** Repeatability ( $r$ ) and associated P-value in foraging and trophic ecology parameters within mates and among random individuals of Cory's shearwaters. Pairs of mates or random individuals were always established between male and female. Tests corrected for Sex (fixed factor), Colony, Year, Individual and Nest (random factors). Significant values are indicated in bold.

	Mates		Random	
	$r$	$P$	$r$	$P$
<b>Trip characteristics</b>				
Trip duration (d)	0.28	0.07	0.18	0.25
Max. dist. to colony (km)	0.42	<b>0.05</b>	0.29	0.11
Sinuosity index	0.22	0.17	0.26	0.14
<b>Spatial Ecology</b>				
95% Kernel UD overlap	0.33	0.09	0.34	0.08
50% Kernel UD overlap	0.55	<b>0.01</b>	0.22	0.16
Area of the 50% Kernel UD	0.45	<b>0.02</b>	0.16	0.29
<b>Habitat foraging areas</b>				
Bathymetry (m)	0.70	<b>&lt; 0.001</b>	0.15	0.27
Sea Surface Temperature ( $^{\circ}\text{C}$ )	0.31	0.11	0.09	0.35
Chlorophyll <i>a</i> concentration ( $\text{mgm}^{-3}$ )	0.69	<b>0.001</b>	0.11	0.30
<b>Trophic Ecology</b>				
Carbon signature plasma ( $\text{‰}$ )	0.64	<b>0.001</b>	0.21	0.17
Nitrogen signature plasma ( $\text{‰}$ )	0.23	0.19	0.19	0.23

Pair members showed a high degree of similarity in several foraging at-sea characteristics (Table V). Namely, the maximum distance to colony, 50% kernel UD overlap, area of 50% kernel UD overlap, bathymetry, Chl *a* of foraging area and carbon isotopic signature from plasma of males were significantly and positively related with those of females (i.e. between mates) (Table V and Figure

6). The proportion of times mates met at-sea influenced significantly and positively the proportion of times they met at the colony (Table V and Figure 7). The proportion of times mates met at their colony had also a positive and significant effect on the mean daily mass variation and the proportion of times mates met at-sea influenced significantly and positively the proportion of nights the chick received food and the mean daily mass variation (Table V and Figure 8).

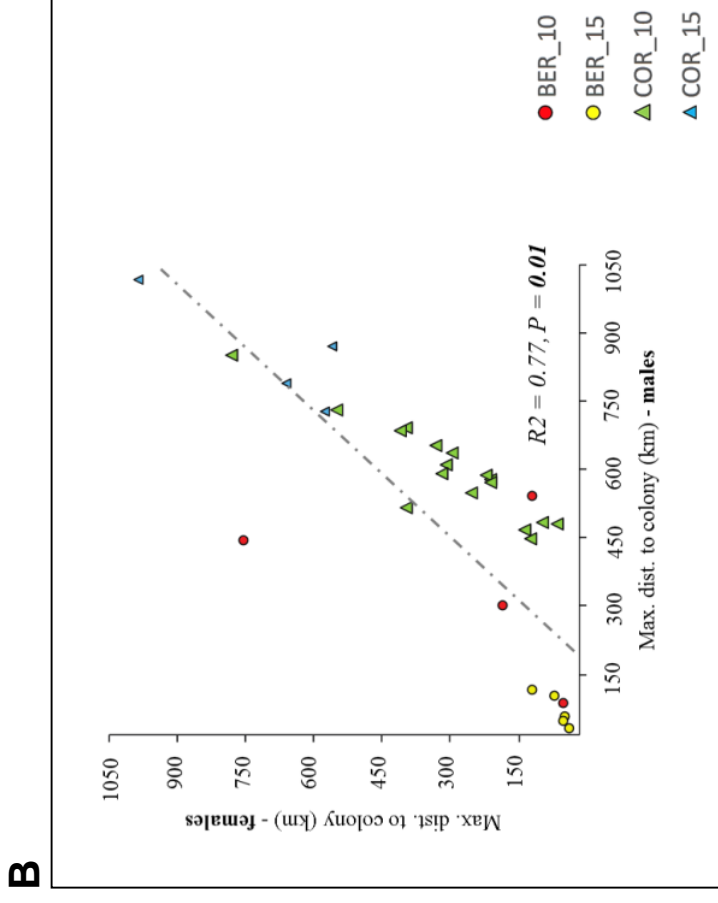
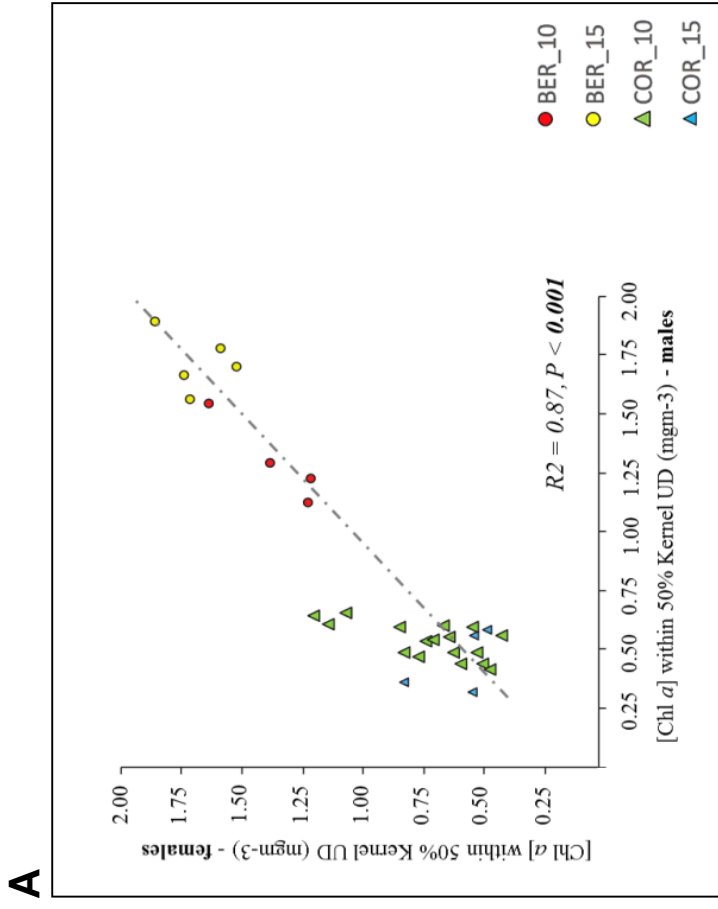
**Table V.** Linear mixed models of relationships between (A) mates foraging at-sea characteristics; (B) at-sea and at-colony behaviour of mates; (C) mates behaviour and parameters of chicks' provisioning and growth. Prop. – proportion. SST – sea surface temperature. Chl *a* – chlorophyll *a* concentration. FA – foraging area, as the 50% kernel UD. N = 32 pairs, 222 foraging trips. Mixed effects models included Sex as a fixed factor, and Colony, Year, Individual and Nest as random factors. Significant differences are indicated in bold.

Independent parameter	Response parameter	$\beta$	SE	t	P
<b>(A) Mates relationship</b>					
Trip duration – male	Trip duration – female	0.08	0.05	1.76	0.12
Max. dist from colony – male	Max. dist from colony – female	0.19	0.09	2.80	<b>0.01</b>
Sinuosity index – male	Sinuosity index – female	0.05	0.10	1.25	0.23
95% Kernel UD overlap – male	95% Kernel UD overlap – female	0.12	0.03	1.20	0.27
50% Kernel UD overlap – male	50% Kernel UD overlap – female	0.25	0.07	2.46	<b>0.02</b>
Area of the 50% Kernel UD – male	Area of the 50% Kernel UD – female	0.29	0.02	2.76	<b>0.01</b>
Bathymetry of FA – male	Bathymetry of FA – female	0.36	0.09	4.46	<b>&lt;0.001</b>
SST of FA – male	SST of FA – female	0.11	0.04	1.35	0.19
Chl <i>a</i> of FA – male	Chl <i>a</i> of FA – female	0.32	0.05	4.69	<b>&lt;0.001</b>
Carbon signature plasma – male	Carbon signature plasma – female	0.29	0.03	2.81	<b>0.01</b>
Nitrogen signature plasma – male	Nitrogen signature plasma – female	0.09	0.04	1.28	0.22

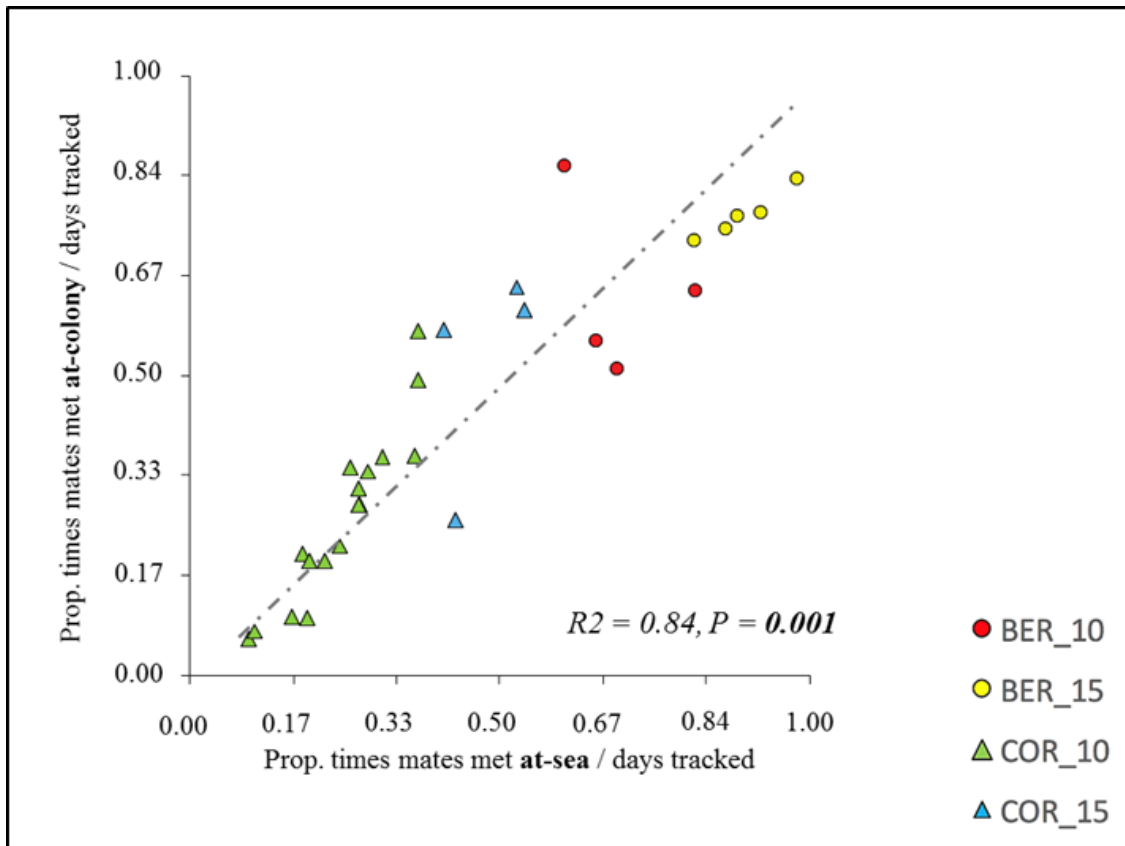
**Table V. (continuation)** Linear mixed models of relationships between (A) mates foraging at-sea characteristics; (B) at-sea and at-colony behaviour of mates; (C) mates behaviour and parameters of chicks' provisioning and growth. Prop. – proportion. SST – sea surface temperature. Chl *a* – chlorophyll *a* concentration. FA – foraging area, as the 50% kernel UD. N = 32 pairs, 222 foraging trips. All mixed effects models included Sex as a fixed factor, and Colony, Year, Individual and Nest as random factors. Significant differences are indicated in bold.

Independent parameter	Response parameter	$\beta$	SE	t	P
<b>(B) Relationship between at-sea and at-colony behaviour</b>					
Prop. of times met at-sea	Prop. of times met at-colony	0.21	0.08	3.69	<b>0.001</b>
<b>(C) Effect of mates behaviour on chicks' provisioning and growth</b>					
Prop. of times met at-colony	Prop. of nights the chick received food	0.12	0.10	1.87	0.08
Prop. of times met at-colony	Mean daily mass variation	0.29	0.09	2.11	<b>0.05</b>
Prop. of times met at-sea	Prop. of nights the chick received food	0.32	0.03	2.89	<b>0.01</b>
Prop. of times met at-sea	Mean daily mass variation	0.35	0.04	2.88	<b>0.01</b>

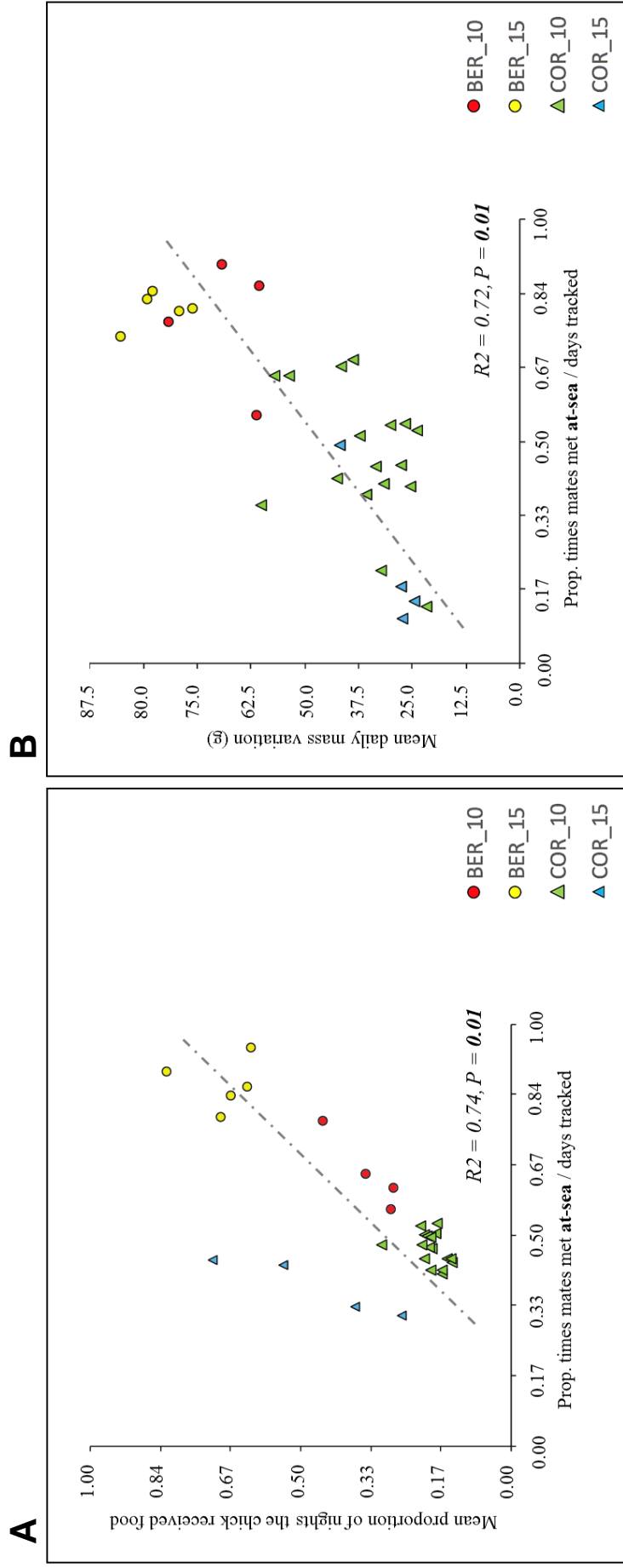




**Figure 6.** Relationship between (A) the chlorophyll *a* concentration (Chl *a*) within the 50% Kernel UD and (B) the maximum distance to colony of habitats exploited by mates from Corvo (COR) and Berlenga (BER) during 2010 (10) and 2015 (15). Also shown in the plots a dashed-dotted line depicting the linear relationship between variables and the regression coefficients with correspondent P-values.



**Figure 7.** Relationship between the proportion of times mates met at-sea and at-colony/ days tracked, for birds from Corvo (COR) and Berlenga (BER) during 2010 (10) and 2015 (15). Also shown in the plots a dashed-dotted line depicting the linear relationship between variables and the regression coefficients with correspondent P-values.

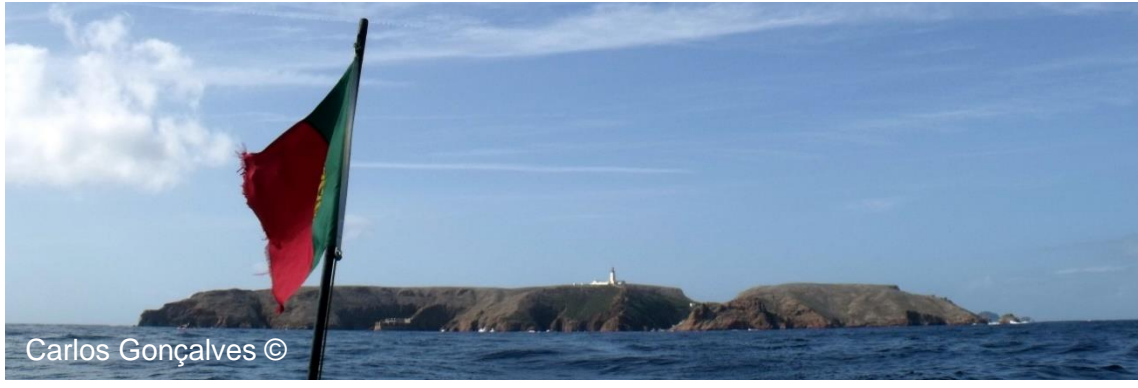


**Figure 8.** Relationship between (A) the proportion of times mates met at-sea/days tracked and mean proportion of nights the chick received food (B) the proportion of times mates met at-sea/days tracked and mean daily mass variation (g). Also shown in the plots a dashed-dotted line depicting the linear relationship between variables and the regression coefficients with correspondent P-values.



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## Chapter 4 – Discussion



*Berlenga Island*



Our results show strong signs of coordination between the pair of Cory's shearwaters, although their behaviour was strongly influenced by the colony where they reproduce, as birds from Berlenga demonstrated higher number of at-sea and at-colony encounters and thus potential coordination than birds from Corvo as we anticipated, i.e. strong differences between neritic and oceanic colonies. In fact, there were significantly higher number of encounters between the two members of the pair at sea and at the colony for Berlenga than for Corvo, and apparently this led to a better regulation of food delivered to the chick in Berlenga than in Corvo. Below we outline the limitations of our study and discuss the implications of our study to the understanding of regulation of procellariiform chick food provisioning between the breeding pair.

#### **4.1 Study limitations**

Our study was innovative as there are virtually no studies documenting the encounters of procellariiform breeding pairs both at sea and at the colony. However, our study has some limitations to consider:

(1) First we do not know the effective interaction between the two members of the pair both at sea and at the colony, for that we would need video cameras. With the GPS data we only have access to positions of each member of the pair, and we can find out when they are together but we cannot observe their behaviour.

(2) It is difficult to evaluate whether higher level of encounters at sea for Berlenga were simply due to a more favourable environment such as rich foraging

grounds and overall favourable ocean and wind conditions (Paiva et al. 2013), thus birds had more free time to meet, or to a decision making process of the individuals.

(3) Another limiting aspect of this work is related with the sample size, which was very variable between years and colonies, because both members of the pair had to be tracked during the same time period.

Nevertheless, other recent studies with different pelagic seabirds support our results. Common Guillemots (*Uria aalge*) in the Baltic Sea adjusted chick provisioning accordingly with the chicks needs (Kadin et al. 2016), in years with lower food quality the pair compensate by increasing feeding rates unlike in years with better food quality. Shojil et al. (2015) suggested that Manx shearwaters coordinate their foraging mode change-over to prevent chicks from being unfed for more than 3 days, disproving the idea that change-overs were initiated when parents reach critical lower body mass. Our evidence of lower coordination in the Azores are in accordance with other studies; e.g. Magalhães et al. (2008) studied Cory's shearwaters in the Azores and suggested that birds did not coordinate their activity to avoid chicks from being unfed during several nights.

#### **4.2 Influence of neritic vs oceanic conditions in pair encounters**

A higher presence of encounters at sea in pairs from Berlenga can be explained by the smaller area used during foraging, because individuals used the same areas of high productivity (i.e. upwelling areas with higher Chl *a* values) near



the colony in the continental shelf (Louzao et al. 2006). In the colony of Corvo the trips of both members of the pair are much longer (Paiva et al. 2010), and the at-sea encounters are less frequent. This is probably related with the different foraging strategies between the two colonies. A dual-foraging strategy, i.e. a sequence of long and short foraging trips is very common in the Azores (Magalhães et al. 2008) but it is almost absent from Berlenga, as we recorded in our study. Also, chicks from Berlenga have shown a shorter fledging period than birds from oceanic colonies of the Azores and Selvagens (Ramos et al. 2003).

The visits to the colony to feed the chick appeared to be directly related with the proportion of encounters at sea between the pair. Even in Corvo, where the proportion of encounters was lower, there was a tendency that with an increased number of encounters at sea there was an increase in the encounters at the colony. This trend was also reflected in the proportion of nights that the chick received food, and the increase in at-sea encounters lead to a higher frequency of chick feeding events. To our best knowledge this is the first time that at-sea encounters between mates is studied and linked to the feeding frequency of the chicks.

It is well known that the foraging strategies in Procellariiformes may change in relation to prey availability in the surroundings of the breeding colony (Congdon et al. 2005). Our results suggest that different foraging strategies mean that food resources are more abundant and available near the coast than near the oceanic colony. Given the less predictability of food resources in oceanic colonies, birds from Corvo could benefit more from the existence of coordination between the mates, in order to feed their chicks and themselves. However, this may be difficult given the long foraging trips and vast ocean areas that birds use. Long trips characteristics from Corvo birds could result in chicks being unfed during several

nights if the pair perform such long trips simultaneously. Wedge-tailed Shearwaters, on the contrary, can reduce the number of nights that the chick is unfed when the two parents apparently coordinate their provisioning through the changeovers (Congdon et al. 2005). The fact that seems to explain better their coordination is that changeovers occur when one member of the pair returns from a long trip and makes contact with the other member probably at sea or at the nest.

Moreover, the mean daily mass variation of chicks was more constant for Berlenga where the at sea encounters were more frequent and coordination appeared to be more effective, meaning that chick growth was presumably related with the coordination between the pair.

#### **4.3 The influence of environmental conditions in explaining pair encounters**

It is important to notice that variable oceanographic characteristics part from the neritic vs oceanic situation should influence the coordination of the pair. In order to control for this our study was made in two years off very contrasting oceanographic conditions. Negative values of the extended winter index (wNAO) in 2010 (-4.6) induced a decrease in productivity in the surroundings of Berlenga which forced birds to forage farther from the colony with greater foraging effort. In contrast, such negative value depicts higher marine productivity in the surroundings of Corvo, with birds performing shorter trips and foraging closer to the colony. In 2015, the wNAO was positive (3.6), i.e. a year of more favourable conditions for Berlenga, where birds only performed short excursions, while Corvo birds performed a comparatively higher proportion of longer trips, both in distance

and duration, as a response to decrease productivity (and likely prey availability) at the colony surroundings. As a result, when conditions are favourable there is a greater potential for encounters at sea and more regular trips to the nest, so adults can better infer about the nutritional status of their young and adjust the food supply accordingly to their needs. On the contrary in less favourable years, or colonies where resources tend to be scarce, encounters are reduced and visits to colony less regular and therefore the nutritional status of the chick is less likely to be taking into account for subsequent feeding events. Therefore, it was important to study the behaviour of this seabird in two different colonies, with distinct oceanographic characteristics to better identify these differences and resemblances.

Knowing that the general conditions are more favourable in the surrounding of Berlenga would be expected that pairs from that colony did not even need coordination, which would be more important in the oceanic colony. One possible explanation for this apparent contradiction is that the favourable environmental conditions allow and facilitate the existence of coordination in that colonies, with an increase in breeding success. On the other hand, where the conditions are less favourable, although the birds would benefit from coordination, they may not be able to achieve it, at least as efficiently as their counterparts in the neritic colony. It is important to emphasize that for both colonies the relationship between bathymetry and 50% Kernel UD overlap were significantly more similar between the mates when compared with random paired individuals. This means that, even in the oceanic colony, there is some coordination between the pair in terms of foraging behaviour.

As expected, the signature of stable isotopes from the plasma revealed that values were more similar between the pair than when compared with other

individuals, confirming that the behaviour of the two individuals is more similar to each other than to other individuals of the population. Müller (2015) obtained similar results in the tracking of the annual migration of Scopoli's shearwaters breeding in Linosa Island (Italy): There were high similarities in the migration parameters between the two members of the breeding pair, which travelled to similar nonbreeding destinations, spent similar number of days traveling and showed smaller distances between nonbreeding areas than other random birds in the colony.

Our findings suggest that when the resources near the colony and general at-sea conditions are favourable, short foraging trips can keep the body maintenance of both chick and adults, and adult birds can coordinate the foraging and chick provisioning. On the other hand, when a dual foraging strategy is common, i.e. in oceanic colonies and during years with unfavourable at-sea conditions (Paiva et al. 2010; Magalhães et al. 2008) coordination is more unlikely to occur.

Originally several studies proposed that food provisioning in pelagic seabirds was mediated by an intrinsic rhythm without taking into account the chick condition (Ricklefs 1992; Hamer and Hill 1993). Harris and Wanless (2011) suggested that in bi-parental care species the foraging coordination between the pair is important to guarantee that the chick requirements are met without over-feeding (Shojil et al. 2015). Our study and other studies suggested more plasticity in the foraging behaviour of pelagic seabirds (Weimerskirch 1995; Tveraa et al. 1998) where adults can adjust the feeding events according to the environmental conditions.

#### 4.4 Social information and coordination between the breeding pair

We connected the at-sea encounters with the presence of coordination between the pair but the mechanism behind the process is still difficult to understand. Similarly to other species, seabirds are able to use social information to adjust their foraging behaviour. Social information is a common phenomenon in nature and the observations of other individuals in the same condition may facilitate taking decisions (Seppänen et al. 2007). Animals benefit from observing others in a foraging context, which is a widespread phenomenon across the animal kingdom (Danchin et al. 2004). For example the Brown Rat use their companions breathe do decide what to eat when they face unfamiliar food. Weimerskirch et al (2010) found that Guanay Cormorants (*Phalacrocorax bougainvilli*) are able to use social information, using the rafts as a compass that indicates the location of food resources. Moreover, the authors suggest that this use of information may be common in central place foragers like our study species. In more recent studies with this same species Weimerskirch et al. (2010) confirmed that Guanay Cormorants use rafts to find out the locations of food patches observing the behaviour of the individuals that return from favourable food patches. Also, in our study, after attending their chick adults returned to the sea and join again the compass raft presumably to gain recent information given by other birds. As a species that spends almost all his life at sea, the use of this information and the ability to transmit information between the pair can be a characteristic of great importance to survive in vast oceanic areas where food distribution is unpredictable (Boyd et al. 2016). In this way, birds would be more likely to avoid areas without

prey. Thus, it is possible that the pair share information about, for instance, areas of higher productivity and seamounts where resources are more abundant. There are several studies regarding the use of social information in seabirds but there is a need to do more research about coordination between the breeding pair. Based on our results, it is possible that the mates follow each other at sea during foraging especially in neritic colonies where they explore a smaller area.

#### **4.5 Concluding remarks**

Our results suggest that Cory's Shearwaters can coordinate their foraging behaviour and regulate the food provisioning in accordance with the needs of the chick, when the at-sea conditions are favourable. Therefore, our results do not fit the idea that Procellariiforms have an intrinsic feeding rhythm (Ricklefs 1992, Hamer and Hill 1993), neither that lipid accumulation is the result of a chronic and unregulated feeding by the adults as suggested by Ricklefs and Schew (1994). However, the idea that this lipid accumulation may serve as a prevention against food shortage periods (Ricklefs 1990) or stochasticity in foraging success of the pair should not be completely ruled out because different colonies and different oceanographic characteristics mean that the coordination between the pair can be difficult to achieve, and thus chick obesity may be crucial to survive in areas and/or years with poor foraging conditions around the breeding colonies. Thus, although the parents adjust their feeding behaviour to be as efficient as possible, this adaptation may serve as a backup for when the parents have no control over the

feeding frequency, and it may be a genetic characteristic that may in some circumstances convey a selective advantage (Bolton 1995a).

For further knowledge about coordination between the breeding pair of pelagic seabirds it would be interesting to apply the same approach in other breeding colonies and other seabird species. Such new studies should use video cameras to document not only the time of arrival and departure of the adults from the nest more accurately, but also register their behaviour at the nest and know when the chick was fed and by which parent. This new technology was used by Thiebault et al. (2014) on Cape Gannets (*Morus capensis*) in Bird Island to study their use of social information and their behaviour at-sea and interactions with the other members of the population.





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## References



*Cory's Shearwaters*



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