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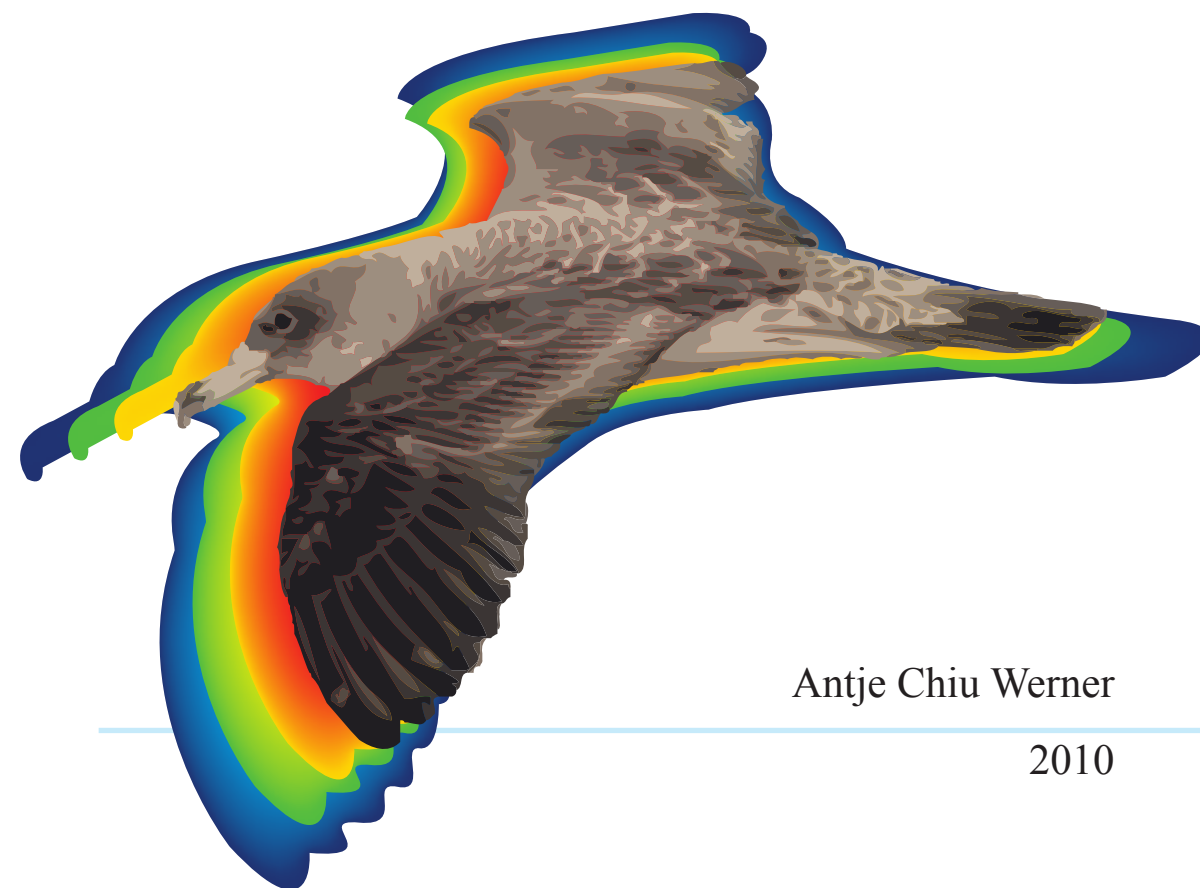
# DEPARTAMENTO DE ZOOLOGIA

FACULDADE DE CIENCIAS E TECNOLOGIA  
UNIVERSIDADE DE COIMBRA

Pre-breeding period in Cory's shearwater: bird quality and foraging behaviour

Antje Chiu Werner

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## Pre-breeding period in Cory's shearwater: bird quality and foraging behaviour

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 A. Ramos (Universidade de Coimbra) e do Doutor Vitor H. Paiva (Universidade de Coimbra)

Antje Chiu Werner

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2010

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## Abstract

1. The pre-breeding period in Cory's shearwater *Calonectris diomedea* is certainly the less studied stage in the life cycle of this species. Yet, it is especially during this period when the purposes of energetic expenditure vary between sexes leading to possible dimorphisms in their foraging ecology. Namely, females will have to cope with the costs of egg production whereas males will engage in nest defense from conspecific competitors.
2. During the incubation and chick rearing period, the foraging ecology patterns are determined by the presence of the egg and later the chick. However, no studies have yet assessed which traits influence the foraging ecology of this species during the pre-breeding period and moreover for each sex.
3. Thus, this study focused on two major aspects that could influence the foraging ecology of Cory's shearwater in males and females during the pre-breeding period: the nest quality and ocean productivity. To do so, nests were characterized by their physical features, previous breeding success and current occupancy rates. On the other hand, 33 individuals (16 females and 17 males) were instrumented with GPS-loggers to record their at-sea behavioural patterns. This data was then analyzed with low and high resolution remote sensing measurements of marine primary productivity (Chl-a, SST and bathymetry) to additionally test for the influence of the resolution of remote-sensing spatial and temporal resolution on the interpretation of behavioural patterns displayed Cory's shearwaters and other marine predators .
4. Results show that male's behavioural patterns are strongly influenced by nest variables associated to quality. Furthermore, this study suggests that the success of males in gaining a proper nest during the pre-laying will define the outcome of the

coming breeding season for that pair, revealing that only high quality individuals will get the chance to breed. Yet, such quality differences within males were not obvious in terms of at sea behavioural patterns and foraging ecology.

Females on the other hand did not show any specific patterns related to nests, however they showed to forage at considerable less productive areas than males during this period suggesting that they might be searching for very specific nutrients rather than prey availability. Furthermore males and females showed to forage in areas that are slightly less productive than the richest areas found within their home range, which suggests that a small mismatch with respect to primary productivity still exists.

Last but not least, the results of this study suggest that the use of low-resolution remote sensing products in combination with highly-accurate tracking devices may lead to Type I errors.

5. Application: The design of marine important bird areas (mIBAS) in the North Atlantic System is strongly based on Cory's shearwaters foraging ecology. Behavioural dimorphisms in foraging ecology of this species during the pre-laying period should be taken into account in the design process as they reveal different patterns and habitat use as during the incubation and chick-rearing period.



## Resumo

1. Na cagarra *Calonectris diomedea* o período pré-postura é certamente o menos estudado de todo o ciclo de vida da espécie. No entanto, é especialmente durante este período que os efeitos do gasto energético deverão variar entre sexos, levando a possíveis dimorfismos na ecologia de forrageamento no mar. Nomeadamente, as fêmeas terão que lidar com o custo energético de gerar o ovo enquanto que os machos se envolverão na defesa do ninho, de outros machos.
2. Durante os períodos de incubação e alimentação às crias, os padrões da ecologia de forrageamento são influenciados pela presença do ovo e mais tarde da cria. No entanto, ainda nenhum estudo avaliou que características poderão influenciar a ecologia de forrageamento nesta espécie durante o período de pré-postura e mais ainda que diferenças existirão entre sexos durante esta fase.
3. Assim, este estudo incidiu sobre dois aspectos importantes que poderão influenciar a ecologia de forrageamento da cagarra em machos e fêmeas durante o período de pré-postura: a qualidade do ninho e a produtividade oceânica. Nesse sentido, os ninhos foram caracterizados de acordo com as suas características físicas, o sucesso de reprodução em anos anteriores e as taxas de ocupação actuais. Por outro lado, 33 indivíduos (16 fêmeas e 17 machos) foram equipados com GPS-loggers para gravar os seus padrões de comportamento no mar. Estes dados foram então analisados com dados de detecção remota de baixa e alta resolução, para medições da produtividade primária marinha (Chl-a, SST e batimetria), de forma a adicionalmente testar a influencia da resolução espacial e temporal dos dados de detecção remota, na interpretação dos padrões comportamentais exibidos pelas cagarra e outros predadores marinhos.

4. Os resultados mostram que os padrões de comportamento dos machos são fortemente influenciadas pelas variáveis associadas à qualidade do ninho. Além disso, este estudo sugere que o sucesso dos machos na obtenção de um ninho adequado na fase pré-postura definirá o resultado desse mesmo período reprodutor para o casal, revelando que apenas os indivíduos de alta qualidade terão a oportunidade de se reproduzir. Contudo, tais diferenças de qualidade entre machos não foram evidentes em termos de padrões de comportamento e ecologia de forrageamento no mar. As fêmeas, por outro lado não apresentaram padrões específicos relacionados com os ninhos, no entanto, mostraram forragear em áreas marinhas consideravelmente menos produtivas do que os machos, sugerindo que as fêmeas poderão estar à procura de nutrientes muito específicos, em vez de disponibilidade de presas. Além disso, tanto os machos como as fêmeas forragearam em áreas que são ligeiramente menos produtivo do que regiões mais ricas encontradas na sua área máxima de distribuição, o que sugere a existência de um pequeno desencontro em relação à produtividade primária. Por último, os resultados deste estudo sugerem que o uso de produtos de detecção remota com baixa resolução em combinação com dispositivos de localização altamente precisos poderá levar a erros do tipo I.
5. Aplicação: O design de áreas marinhas importantes de aves (mIBAS) no Atlântico Norte é fortemente baseado na ecologia de forrageamento da cagarra. O dimorfismo comportamental na ecologia de forrageamento desta espécie existente durante o período pré-postura deverá ser tomado em conta no processo de design, já que os indivíduos revelaram diferentes padrões no uso do habitat daqueles descritos para os períodos de incubação e alimentação às crias.

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## PRE-BREEDING PERIOD IN CORY'S SHEARWATER: BIRD QUALITY AND FORAGING BEHAVIOUR

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### **General introduction**

The order Procellariiformes (tubenose birds) includes most pelagic birds which are also among the most long-lived birds (Bried et al., 2003). Their reproductive cycle is characterised by the laying of a single highly nutritious egg per breeding attempt and the occurrence of a short exodus in females – and sometimes in males – from the breeding area immediately before the egg-laying period (Warham, 1964; Warham, 1990). Because they sit on top or near the top of most marine food chains they are often considered important ecological indicators of changes in the marine ecosystem (Boyd et al., 2006; Furness and Camphuysen, 1997; Gonzalez-Solis and Shaffer, 2009; Montevecchi and Myers, 1996; Parsons et al., 2008) even at an integrative scale (Jenouvrier et al., 2003). Yet, some critics exist around the fact that seabirds are often identified as monitors and indicators by making a relative and generalized use of behavioural and demographic measurements without previously testing the feasibility and usefulness of this species as such (i.e. the level of sensitivity or resilience of each species given particular levels of change) (Durant et al., 2009; Einoder, 2009).

The Cory's shearwater *Calonectris diomedea* is one of the most representative Atlantic seabird species with a large population size estimated in 600 thousands to 1.2 million individuals (BirdLife, 2009). It has a wide foraging and breeding range (in the sub-tropic North-East Atlantic, in the Mediterranean and on Cape Verde), mostly dependent on the variability of seasonal patterns (e.g. food/prey availability, breeding phenology) (Amorim et al., 2009). Their flight strategies and migration routes are well

documented (Felicísimo et al., 2008; Gonzalez-Solis et al., 2007; Gonzalez-Solis et al., 2009; Paiva et al., 2010; Ristow et al., 2000), yet the information on its foraging ecology and behaviour is highly biased towards the breeding period e.g. (Catry et al., 2006; Catry et al., 2009; Gomez-Diaz and Gonzalez-Solis, 2007; Granadeiro et al., 1998a; Granadeiro et al., 1998b; Granadeiro et al., 1998c; Magalhaes et al., 2008; Mougin and Mougin, 1998; Mougin et al., 2002; Navarro and Gonzalez-Solis, 2009; Navarro et al., 2009). Even so, this species has become an umbrella species as the relative recent creation of Marine Important Bird Areas (mIBAS) (an extension of the Important Bird Areas [IBA] approach in terrestrial and freshwater ecosystems by BirdLife) in Portugal (Ramírez et al., 2008) and Spain (Arcos et al., 2009) is greatly based on the knowledge of the life-history of this species.

Especially in this context, the scarce available information on foraging behaviour and ecology during the pre-laying period turns relevant. The pre-laying period comprises the time between the arrival to the breeding ground and the laying of the egg. In Cory's shearwaters it lasts approximately 90 days, from the end of February and beginning of March to the end of May and beginning of June (Mougin et al., 2000). This period represents a crucial time for seabirds as individuals have to feed up to recover the energy lost during migration while assessing nest and partners conditions (Warham, 1990). Furthermore, it is during this period in which males and females adopt different behavioural strategies as their temporary goals are also different: namely males engage mostly in guarding the nest from conspecific intruders (Monteiro et al., 1996; Ramos et al., 1997) while females support the energy costs of egg production (Granadeiro et al., 1998a; Jouanin et al., 2001). Thereafter, the energetic investment of males (i.e. fat reserves) during the pre-laying period is much higher than in females, losing as much weight as females gain in mass by the end of this period (Mawhinney et

al., 1999). Therefore, the quality and availability of food plays a very important role at a population and individual level as it frequently affects the reproductive success of seabirds (e.g. Marbled Murrelet (*Brachyramphus marmoratus*) (Becker and Beissinger, 2006), Cassin's auklets (*Ptychoramphus aleuticus*) (Sorensen et al., 2009)). Nevertheless, studies in the short-tailed shearwater *Puffinus tenuirostris* (Bradley et al., 2000), Grey-headed Albatross *Diomedea chrysostoma* (Cobley et al., 1998) and also Cory's shearwaters *Calonectris diomedea* (Mougin et al., 2002) have found that reproductive performance depends also on individuals' quality and might be independent of the environment or age of the individual.

This study was carried out at Berlenga Island, the largest of a group of three rocky islets (Berlenga, Estelas and Farilhões) just off the Portuguese coast, on the continental shelf. This archipelago is recognized as an IBA and is surrounded by high productive waters. Male and female Cory's shearwaters were tracked using GPS data loggers attached to the contour feathers on their back from the 10 of April to the 10 of May 2010 covering the middle third of the pre-laying period in this species.

To assess for the intra-specific variation in terms of individual quality, this study evaluated the differences in foraging behaviour related to nest characteristics, especially in males (Chapter 1) and the differences of at-sea foraging patterns between individuals related to environmental variables (chlorophyll-a [chl-a] concentrations, sea surface temperatures [SST] and bathymetry [depth]) (Chapter 2). Moreover, Chapter 2 uses Cory's shearwater as an example to assess the influence of the spatial resolution of remote sensing products on the interpretation of the use of marine environments by different species. Each chapter is preceded by an introduction dealing in more detail with each approach.

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## **CHAPTER 1**

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## DOES THE INTRINSIC VARIATION OF NESTS INFLUENCE THE AT-SEA BEHAVIOUR OF CORY'S SHEARWATERS DURING THE PRE-LAYING PERIOD?

---

### **Introduction**

In many territorial species, the quality of territory is directly associated to the reproductive success of the couple, dominant individuals generally getting access to territories with better quality resources. In animals such as seabirds, the central place foraging model (Orians and Pearson, 1979) predicts that parents should select territories (i.e. nest location) that will optimize prey delivery to the chicks by minimizing travelling distances to the foraging patch (e.g. Naef-Daenzer, 2000), which, for many seabird species is situated far out at sea (Cairns, 1989; Elliott et al., 2009; Wittenberg and Hunt, 1985).

Established seabird breeding colonies often result in social attraction of conspecific individuals seeking for a place to nest (Kildaw et al., 2005). This would suggest that costs such as the competition for resources like nest-sites (Ramos et al., 1997) or food (Furness and Birkhead, 1984; Lewis et al., 2001) or the prevalence of parasites are paid-off by the potential benefits of group nesting. Thus, it is often proposed that the size of the colony is related to the productivity of the surrounding ocean (Cairns, 1989; Elliott et al., 2009; Lewis et al., 2001), although for small colonies and far-ranging species such as petrels and shearwaters this may not be the case (Gaston et al., 2007).

Another aspect that many theories aim to explain is the selection of aggregations within colonies of seabirds (A review can be found at Clode, 1993). Yet, the principles proposed are similar to the ones explaining the occurrence of breeding colonies themselves. Ward and Zahavi (1973) and Zahavi (1996) suggested that aggregations work as information centres to gather knowledge on the location of food sources between unrelated individuals. This 'Social Information Centres' theory assumes that the patchily distributed prey of pelagic feeders increase the costs of foraging activities when compared to neritic feeders. Hence, an individual could benefit from evaluating (and be evaluated by) its neighbours for their foraging success and reduce its (food) search time by following them (Buckley, 1997; Burger, 1997; Clode, 1993).

The development of several bird satellite tracking devices (Jouventin and Weimerskirch, 1990; Wilson et al., 2002), namely the Global Positioning Systems devices (hereafter termed GPS-loggers) (Steiner et al., 2000; von Hünenbein et al., 2000; Weimerskirch et al., 2002) have notably increased the amount of information on the behaviour of seabirds (Burger and Shaffer, 2008). These devices have been improving in miniaturization and accuracy (see reviews by (Burger and Shaffer, 2008; Wilson et al., 2002)) and are nowadays accessible at considerable lower prices. Thus, to guarantee the recovery of devices and data, studies have been heavily biased towards the incubation and chick rearing period when most seabirds become central place foragers e.g. (Catry et al., 2006; Catry et al., 2009; Gomez-Diaz and Gonzalez-Solis, 2007; Granadeiro et al., 1998a; Granadeiro et al., 1998b; Granadeiro et al., 1998c; Magalhaes et al., 2008; Mougin and Mougin, 1998; Mougin et al., 2002; Navarro and Gonzalez-Solis, 2009; Navarro et al., 2009; Paiva et al., 2010a; Paiva et al., 2010b) but see Granadeiro et al (1998b), Jouanin et al (2001), Mougin et al (2000a), Navarro et al (2007). The latter represent the only studies that report data corresponding to the pre-

laying period in Cory's shearwater and were based on monitoring the attendance cycles at the colony (Granadeiro et al., 1998b; Jouanin et al., 2001; Mougin et al., 2000a) or using low accuracy devices such as geolocators (Global Location Sensing, GLS) (Navarro et al., 2007) with an average accuracy of 186km (Phillips et al., 2004).

The pre-laying period is crucial to Cory's shearwater and other pelagic seabirds because individuals have to refill the reserves lost during migration while assessing the conditions of their nest-site and mate (Warham 1990). Moreover, it is during this period where sexual behavioural dimorphism is expected to occur since males have to guard the nest during the time in which the female gathers sufficient energy to afford egg production (Granadeiro et al., 1998b; Jouanin et al., 2001). The pre-laying period in Cory's shearwaters lasts approximately 90 days (Mougin et al., 2000a). It starts with the arrival of both individuals to the colony (by the end of February and beginning of March (Monteiro et al., 1996)) and ends when the egg is laid (between end of May and beginning of June) (Mougin et al., 2000a). Cory's shearwaters' first nesting attempts occur at an average age of 9 years (Mougin et al., 1992). From this point, they not only show increasing mate fidelity (Mougin et al., 2000b; Mougin et al., 1999) but also high nest fidelity (Mougin et al., 2002; Thibault, 1994) and philopatry (da Silva and Granadeiro, 1999; Mougin et al., 1999; Rabouam et al., 2000). As a socially monogamous species, migration usually leads to a high synchronization of their behaviours upon arrival to the colony (Gunnarsson et al., 2004). However, apparent laying synchrony in this species does not seem to be a product of a real synchrony with its neighbours but rather a product of the individual's and nest quality (Catry et al., 2006). Thus, competition for nests exists (Monteiro et al., 1996; Ramos et al., 1997) and inexperienced birds often lose nesting sites and become more susceptible to breeding failure (Mougin et al., 2002).



Consequently, if nests with different quality exist within a colony, it is to expect that they influence the behaviour of the individuals at sea (especially males) aiming to compete for that special nest during the pre-laying period (i.e. influence their foraging time, maximum foraging trip distances and other relevant at-sea behavioural parameters). So far, many studies have successfully built artificial burrow nests to translocate different seabird species (e.g. Miskelly et al., 2009) or to increase the number of available nests in a colony (e.g. Bolton et al., 2004). However, because most of these artificial nesting chambers are uniform in each study, no assessment of the intrinsic variation of nests was necessary to explain birds' choices of preference. Moreover, no study has yet attempted to link nest-site features with behaviour at sea.

This study aims to (i) assess whether a considerable variation among nests exists in the colony of Cory's shearwaters breeding on the island of Berlengas, west coast of Portugal (ii) identify the main variables responsible for such variation, (iii) determine if this variation is an indicator of nest quality and, (iv) assess whether these variables have an influence on the at-sea behaviour of Cory's shearwaters. Because males have an active role in nest defence, their at-sea behaviour might vary with the variation of nest variables (or combinations of them) responsible for nest quality. For instance, foraging segregation is expected. Males should be foraging closer to the colony than females as they are restricted by guarding duties, which ought to be directly related to the size of foraging area and the duration of each trip. Furthermore, better quality nests should also condition the behaviour of males (and possibly females) by keeping them foraging closer to the colony.

## **Methods:**

### Study area and Bird count

The archipelago of Berlengas is formed by 3 groups of islands (Berlenga, Estelas and Farilhões, Figure 3) and surrounded by rich feeding grounds as a result of the combination of bathymetric features with ocean and wind circulation. Currently, this archipelago hosts around 850 breeding pairs of Cory's shearwaters: 500-550 pairs nesting in Farilhões and approximately 300 nesting in Berlengas (Miguel Leqoc, *pers. comm.*). This study was carried out on Berlenga Island (39.413611N, -9.508056E) between the 10 April – 10 May 2010. The study colony is situated on the eastern side of the "Old Island" of Berlenga (39.413937N, -9.504926E) where approximately 130 pairs of Cory's shearwater nest in rock crevices, burrows and (mostly) artificial nests. Artificial nest only differ from natural nests in the fact that the rocks forming the nests walls were piled up by people. Most of the birds in this colony had been ringed in previous years and reproductive success data was available for breeding individuals in years 2005, 2006 and 2007 for each nest (V. Paiva, *unpub. data*). Daily censuses of nest occupancy were performed at the colony at around 23h and nest owners were identified every 6<sup>th</sup> or 7<sup>th</sup> day to avoid excessive disturbance. In addition nest occupancy censuses were carried out at day-time every second day. Laying success (presence absence of an egg) for all nests was registered on June 7<sup>th</sup> and on the 1<sup>st</sup> of July. The first date representing almost the end of the egg laying period (Mougin et al., 2000a) whilst the second date was used as a proxy of parents' quality as less successful birds could have lost their egg by then. Accordingly, all nests were carefully checked for abandoned eggs and/or traces of predation.

## GPS tracking devices

CatTaq Travel Loggers (Perthold Engineering LLC) were employed as GPS-loggers. This 44.5 \* 28.5 \* 13mm device weights 20g and contains a SiRF StarIII chipset, a patch antenna, a 230mAh Lithium-ion battery and offers accuracy up to 10m. We removed the plastic case and replaced it by a 7cm long thermo-retractile rubber sleeve, which was then sealed with heat reducing the total weight to 17g (figure 1a). Loggers weight represented between 1.6% and 2.6% of the birds weight which has been suggested to not have a negative effect on the instrumented seabird (Phillips et al., 2003).

Loggers were set to record data (geographic position, altitude, ground speed, course, distance) every 5 minutes from 05h to 22h when birds are more likely to be foraging at sea whilst at night, during the pre-laying period, they are commonly found ashore and inside nests (Granadeiro, 1991; Granadeiro et al., 2009). This way, battery loss was avoided in devices trying to acquire satellite data from inside the crevices. Birds were captured during the night at their nest sites, weighted and individually identified by their ring numbers. GPS loggers were then attached using Tesa\_tape®4651 to the contour feathers along and in between both scapulas avoiding troubling neck movements and covering the uropigial gland (Figure 1b-c). As an extra security measure we glued the tips of each tape stripe used to attach the logger. Total handling time did not exceed 10 minutes and birds were released immediately after.



Figure 1. Process of logger deployment. (a) Logger preparation; (b) loggers' attachment location on the bird; (c) instrumented bird.

A total of 40 GPS loggers were attached to 18 males and 22 females. Individuals that had shown successful nest occupancy (and breeding success) in previous years were preferred to increase the probability of logger recovery. We recovered 38 GPS loggers two of them had been damaged by the bird and had entered in contact with seawater. Other two did not record any data and one only recorded data for the first 3 hours. Ultimately data from 33 loggers (17 males and 16 females) were available after retrieval and used for further analysis. In addition, blood samples (approximately 1.5ml) of each instrumented bird were taken from the brachial vein after logger recovery for testing haematocrit (percentage of packed blood cells in the blood sample) as a proxy of the individuals' quality.

## Nest characterization

A total of 90 nests were characterized in terms of physical features and their relative position in relationship to the overall nest distribution in the colony (Table I). In addition, temperature and relative humidity were recorded using five LOG32 data-loggers. For this purpose a pilot nest characterization was made (Appendix 1) to group nest that were significantly similar in both variables (Spearman  $r > 0.7$ ,  $p < 0.05$ ). Once these groups were established, LOG32 data-loggers were set to register data every five minutes and placed randomly between nests of different groups every 48 hours.

## Data analysis

### *GPS tracking data*

Birds carried the GPS-loggers for different periods of time, mostly dependent on the presence of the bird at the colony (for recapture) and battery duration. To standardize the sampling effort for each bird each foraging trip duration data was divided by the number of days the logger was actively recording on the instrumented bird (up to the minute when battery run off before logger recovery: 1 logger working day = 17 hours). For each instrumented bird, an individual foraging trip was considered as starting and ending at the colony (39.413937N, -9.504926E). Trips were then divided into short (1 day) and long trips ( $\geq 2$  days) by assessing the histogram of the frequency of trip durations (Figure 2a). Overall trip sinuosity was calculated by dividing the maximum trip distance by the cumulative distance of each trip. Maximum trip distances (meters), home range areas ( $m^2$ ) and percentage probability kernels<sup>1</sup> were calculated in

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<sup>1</sup> An X% kernel defines the area around a specific point (i.e. colony) in which an animal can be found with an X% of certainty. Kernel density estimators are commonly used as home range estimators and “consist of placing a probability estimator over each observation point in a sample” Seaman D.E.,

ArcView 3.2 under Alberts Equal Area Conic Projection using the Animal Movement v2.04 extension (Hooge and Eichenlaub, 1997) for each trip. This projection was selected to control for both distance and area measurements (Pinaud and Weimerskirch, 2005). Percentage of at ocean flying time ( $\geq 9$  km/h) versus no-flying time ( $< 9$  km/h) was calculated based on the speed (km/h) frequencies histogram (Figure 2b). Finally mean values of each variable were calculated for each of the 33 individuals.

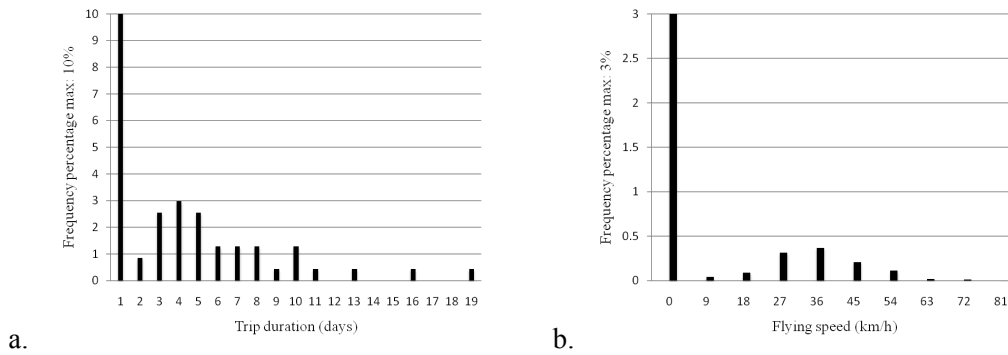


Figure 2. Frequency histograms for (a) trip duration and; (b) flying speed determining break points at 2 days and 9km/h respectively. Percentages were maximized to 10% (a); and 3% (b) for better visualization

The resulting set of variables (Table II) was introduced into CANOCO software (Version 4.5) and a Principal Component Analysis (PCA) focused on inter-sample distances was performed to assess possible sexual behavioural segregation. Mann-Whitney U test was used to assess the level of significance between the differences in male and females' behaviour.

### *Nests characterization*

A factor analysis was performed in STATISTICA (StatSoft, Inc. [2004]), version 7 for the variables of all the nests in the colony (n=90). The resulting factors were then introduced into CANOCO and a PCA with focus on inter-sample distances was performed on the nests where instrumented birds were registered (n=30). At-colony behavioural variables (Table I) were included as species values. These variables were used as a proxy of nest quality under the assumption that higher quality nests will have higher occupation rates during the night and during the day. At night most individuals are at the colony and it is expected that one or two individuals will occupy most nests. However, during the day, most individuals are foraging at sea. Hence, staying to guard the nest during the day represents a sacrifice a bird is willing to take to not lose that nest as suggested by Brooke (1990) in Manx shearwaters *Puffinus puffinus*. The number of different individuals registered at the nest could be interpreted in two opposite ways. It could be assumed to be an indicative of poor guarding behaviour, yet it could also be an indicative of more individuals being interested in that specific nest.

Two approaches were then used to select the (i) group/combination of variables or (ii) individual variables that could explain the behaviour recorded at sea:

- i. The factor scores of the first two principal components (PC) were correlated using Spearman correlations against behaviours recorded at-sea for males and females to assess which behaviours expressed by each bird group were related to the gradient of variation represented by each PC. Significant Spearman correlations ( $p \leq 0.05$ ) reduced the number of principal components to  $N = 1$  and at-sea behavioural variables to  $N = 6$ .

- ii. Individual raw nest variables were directly correlated to behaviours at sea in males and females using Spearman correlations to evaluate which variables were related to the behaviours expressed at sea. Significant correlations ( $p \leq 0.05$ ) reduced the number of at-colony explanatory variables to  $N = 3$  for each sex and at-sea behavioural variables to  $N_{\text{males}} = 5$  and  $N_{\text{females}} = 4$ .



Table I. List of nests' characterization variables (at-colony explanatory variables) and nests' bird behaviour related variables

	<b>Unit</b>	<b>Variable description</b>
<b>At-colony explanatory variables</b>		
Tvar	°C	Nests' temperature variation along study period
Hvar	%	Relative humidity variation along study period
Area_ent	Cm	Nests' entrance area
Depth	Cm	Nests' depth
Altitude	Cm	Nests' chambers height
Width	Cm	Nests' chambers width
Slope	Degrees	Nests' inclination
Orientation	Degrees	Nests' orientation in relation to the North (0°)
%EM	%	Extra nest material
rock	%	Floor substrate - rocks
small_rocks	%	Floor substrate - small rocks
soil	%	Floor substrate - soil
Dist.clos.Neigh	Cm	Distance to closest neighbour
Dist_escape	Cm	Distance to escape platform
<b>At-colony behavioural variables</b>		
N_Occupancy	Integer	Nests' night occupancy rate
D_occupancy	Integer	Nests' day occupancy rate
#ind_nest	Integer	Number of different individuals registered in each nest
Lay success 2010	Integer	Presence/absence of an egg in nest in year 2010

Table II. List of behavioural variables recorded at sea on instrumented birds. Each variable was separately calculated for Long (var\_L) and Short (var\_S) trips (represented by “X”)

<b>At-sea Variables</b>	<b>Unit</b>	<b>Description</b>
mX_trip_dur	Days	Mean duration of long/short trips
mX_maxTrip_dist	M	Mean maximum trip distance of long/short trips
mX_cum_dist	M	Mean cumulative distance in long/short trips
mHR_X	m <sup>2</sup>	Mean home range area of long/short trips
m95K_X	m <sup>2</sup>	Mean 95% probability kernel area for long/short trips
m75K_X	m <sup>2</sup>	Mean 75% probability kernel area for long/short trips
m50K_X	m <sup>2</sup>	Mean 50% probability kernel area for long/short trips
m25K_X	m <sup>2</sup>	Mean 25% probability kernel area for long/short trips
%X_FT	%	Mean percentage of flying time in long/short trips

Finally a PCA for individual quality proxies (Table III) was performed to assess whether the nests distribution along a gradient of individual quality follows a similar distribution pattern as when using at-colony environmental and behavioural data.

Table III. List of variables employed as proxies of bird quality.

<b>Variable</b>	<b>Unit</b>	<b>Description</b>
Hematocrit	%	Percentage of packed blood cells in the blood sample
Mean weight	g	Individuals weight
Breeding success	integer	Total number of fledglings in year 2005, 2006 and 2007
Age	years	Minimum age of the bird in year 2010

The age estimate of each bird indicates that the bird is no younger than the number of years it has been assigned. Minimum bird age calculation was based on the date the bird was ringed (most birds in the colony were not ringed as chicks) and the age code assigned in that year according to the classification given by Euring (Appendix 2). Euring classification is followed by CEMPA (Centro de Estudo de Migrações e Protecção de Aves), the ICNB (Instituto da Conservação da Natureza e da Biodiversidade) dependence responsible for ringing birds in Portugal. In concordance with this, age equal to zero indicates unknown age ( $N_{\text{age}=0} = 10$ ;  $N_{\text{total}}=33$ ). The mean weight was calculated as the average between the weight registered at the beginning of the study (when GPS-loggers were attached to the bird) and the end of the study (when GPS-loggers were retrieved from the bird).

## **Results**

### GPS tracking data

A total of 236 trips were recorded. A PCA of at-sea variables calculated for each individual (Table II) suggested sexual behavioural segregation (Figure 3a). Males showed to have an average trip duration of 1.31 days ( $N=163$ ) while females foraging trips lasted 3.10 days in average ( $N=73$ ). Furthermore, overall trip duration was positively correlated to the size of foraging area ( $N=236$ , Spearman  $R = 0.605$ ,  $p<0.001$ ). Average foraging distances from the colony were significantly greater for females than for males ( $N = 236$ ,  $U = 4119.00$ ,  $p=0.0001$ ) and so where the sizes of foraging areas used at sea ( $N = 236$ ,  $U = 4216.00$ ,  $p=0.003$ ) (Figure 3b). Males also showed to spend less time flying (38%) during their foraging trips than females (45.3%).

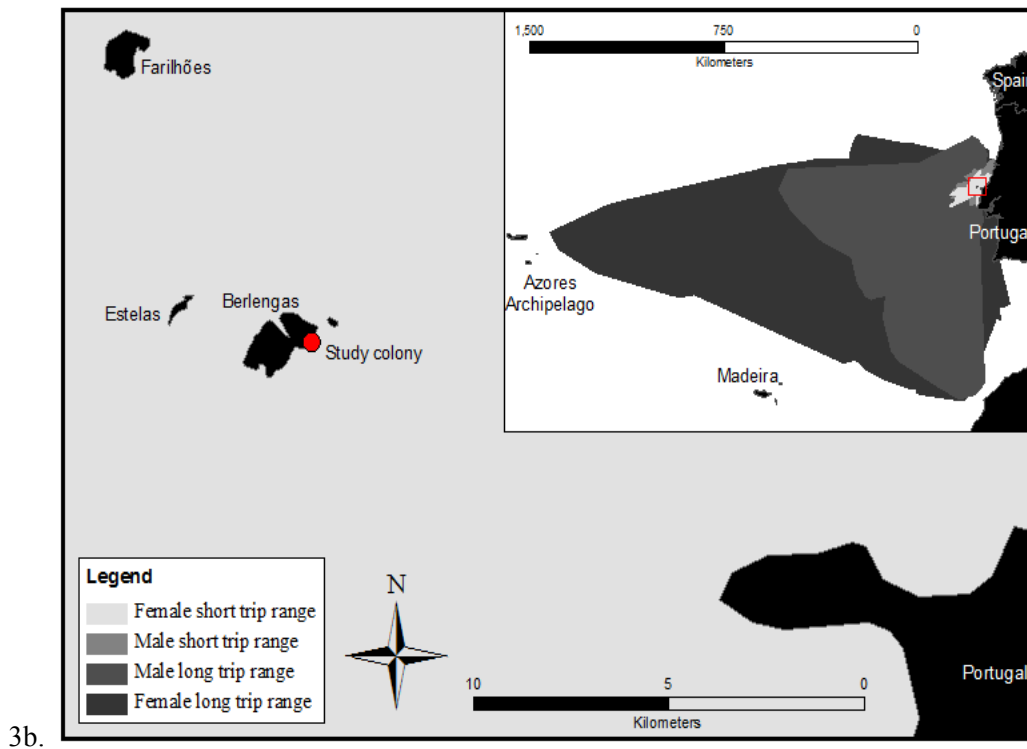
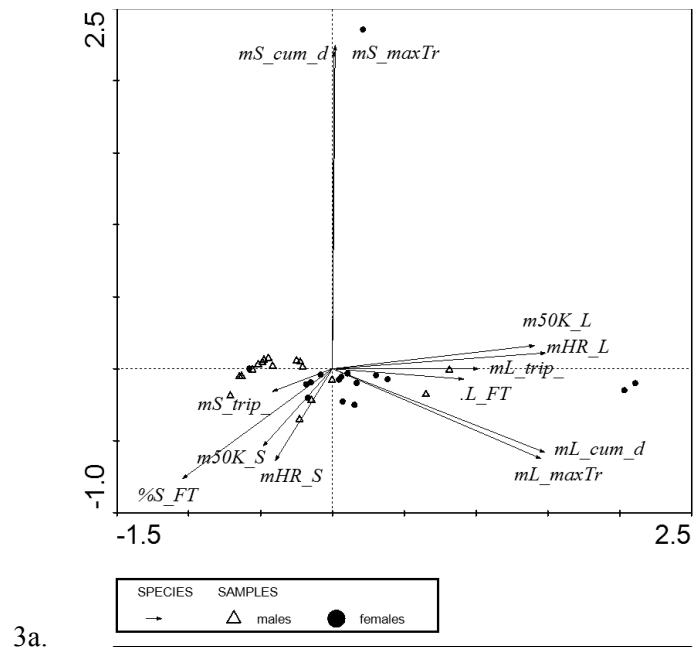


Figure 3. Behavioural segregation between males and females. (a) multivariate analysis (PCA) representation; (b) differences in size of foraging areas between males and females.

For further analyses, histogram of trips' duration frequency suggested to separate short trips (1 day) and long trips ( $\geq 2$  days) (Figure 2a). Break point speed to

separate at-sea flying birds from not-flying birds was calculated in 9km/h from the speed frequency histogram (Figure 2b).

#### Nest characterization

A PCA focusing on inter-species correlations of the behavioural variables used as proxy for nest quality showed that all four of these variables co-vary among them (Figure 4). This suggests that the number of individuals registered per nest is rather an indicator of more birds being interested in those nests instead of a poor guarded nest. In fact, nests less appealing to birds and with lower occupancy rates during the pre-laying period were those where an egg could not be found during both checks in the incubation period.

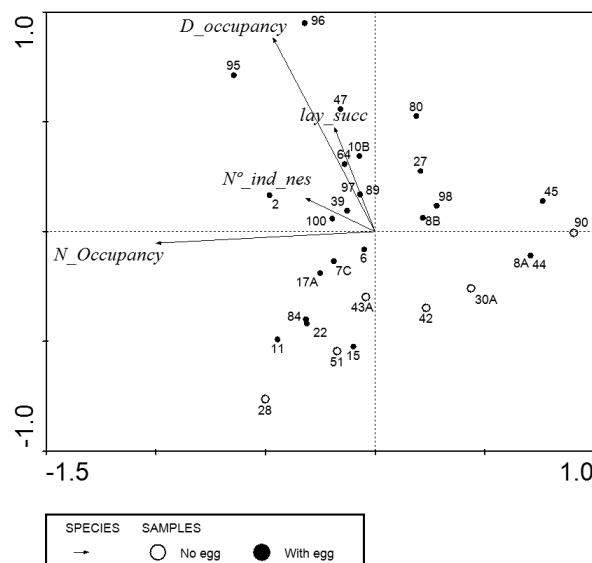


Figure 4. PCA focused on inter-species correlations showing nest distribution along a gradient of quality proxies (species) (e.g. laying success in 2010).

Factorial analysis reduced the number of at-colony explanatory variables from N=14 (Table 1) to N=8 (*Tvar*, *Hvar*, *Area\_ent*, *Chamber height*, *Small\_rocks*, *soil*, *rock* and *%EM*) distributed within five factors. The PCA analysis of these 8 variables (Figure

5) suggested 3 groups of nests based on the birds' at-colony behavioural variables (Table I) used as proxy for nest quality.

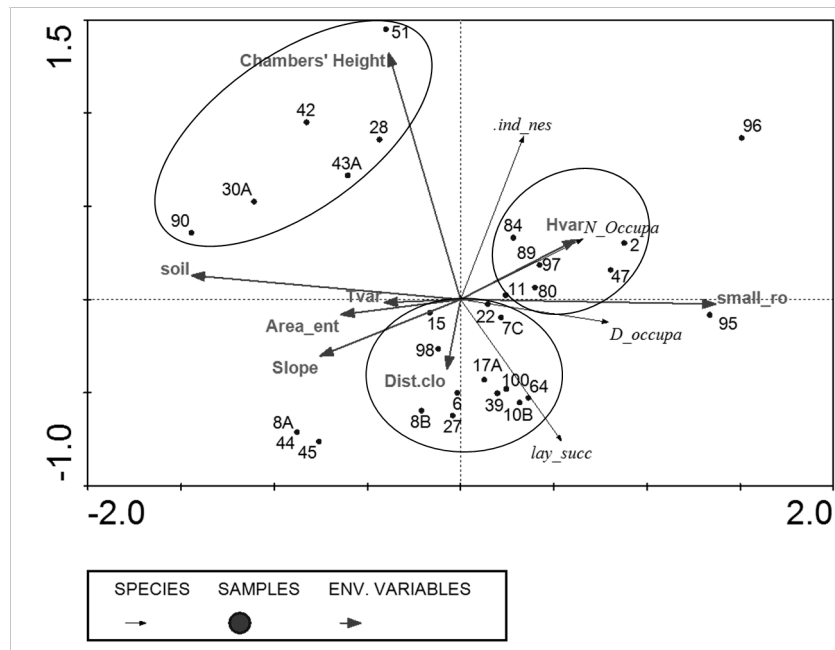


Figure 5. PCA focused on inter-sample distances, where nests' distribution is dependent on the environmental variables best explaining nest variation (N=8) based on proxies of nest quality (species).

From the pattern observed in the PCA analysis (Figure 5), the first principal component (PC1, eigenvalue = 0.45) seems to represent a gradient of nest success where increasing amounts of temperature variation (Tvar), slope, entrance size (Area\_ent) and amount of soil in the substrate (soil) relate to decreasing success of nests in Berlenga. On the other hand, it appears that higher variations in humidity as well as a substrate based on small rocks are related with higher quality nests (PC1). The second principal component (PC2 eigenvalue = 0.32) is greatly represented by the chambers' height (Altitude) and to some extent of humidity variation (Hvar). Moreover, it suggests that higher chambers (= large nest cavities) are related with lower nest quality (PC2). Significant Spearman correlations were found only between the factor scores of PC2 and at-sea behavioural variables for males (Table IV). Furthermore, the male behavioural variables that significantly correlated with the scores of PC2 were highly

correlated between themselves (Spearman  $R \geq 0.85$ ,  $p \leq 0.01$ ). The positive correlations between PC2 and long trip related variables suggest that longer trips and greater foraging areas in males during the pre-laying period are related to poorer quality nests.

Table IV. Significant Spearman correlations (N = 17) between PC2 and at-sea behavioural variables of males

	Spearman R	p-level
PC2 & mL_trip_dur	0.58	0.014
PC2 & mL_cum_dist	0.47	0.057
PC2 & m95K_L	0.52	0.039
PC2 & m75K_L	0.53	0.030
PC2 & m50K_L	0.53	0.030
PC2 & m25K_L	0.53	0.030

Females at-sea behaviour on the other hand showed only a significant negative correlation between PC1 and the percentage of flying time in short trips (Spearman  $R = -0.591611$ ,  $p = 0.015$ ). This suggests that females of higher quality nests might be foraging closer to the colony, because their time looking for food (=flying time) is lower.

On the other hand the correlations between the behaviour of males and females against the nest features suggest that nest variables such as the size of the nests' entrance and the closeness to neighbours condition males' behaviour to short trips (Table V).

Table V. Significant Spearman correlations ( $N_{\text{males}} = 17$ ,  $N_{\text{females}} = 16$ ) between nest features and behaviour of males and females at sea.

	Spearman R	p-level
males		
Area_ent & m95K_S	0.53	0.027
Area_ent & %S_FT	0.50	0.043
Width & %S_FT	-0.62	0.008
Dist.clos.Neigh & m95K_S	-0.53	0.029
Dist.clos.Neigh & %S_FT	-0.54	0.026
Females		
Hvar & m95K_S	-0.54	0.032
Hvar & m95K_L	0.54	0.029
Slope & mL_maxTrip_dist	-0.62	0.010
Dist.clos.Neigh & m50K_S	-0.60	0.014

Females' behaviour on the other hand does not seem to be constrained to short foraging trips. Yet, females foraging over larger areas may be related to nests with chambers where higher variations in the relative humidity occur. Furthermore females' trip distances and size of foraging areas also seem to increase in relation to an increase in distance between their nest and its neighbours (Table V). A PCA focused on inter-species correlations of the quality proxies for males and females also suggested a separate interpretation of results for both sexes (Figure 6).



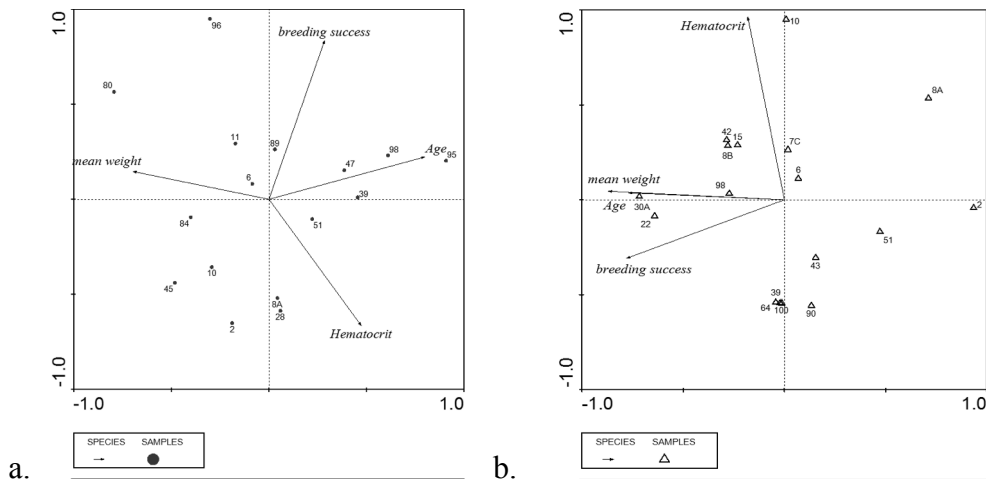


Figure 6. PCA of proxies of individual quality. Samples represent the owners of the labelled nests (a) females (N=16); (b) males (N=17).

For instance, in females the first axis (PC1, N = 16, eigenvalue = 35.7%) represents a gradient of age and weight that go in opposite directions indicating that both proxies are not correlated (Figure 6a). In males instead, age and weight are also represented in the first axis (PC1, N = 17, eigenvalue = 49.8%) but are highly correlated. Furthermore, the breeding success in previous years (= bird experience) also correlates to age and weight of males (Figure 6b). The second axis in females (PC2, N = 16, eigenvalue = 30.3%) once again is represented by a gradient of hematocrit that is opposite to breeding success, suggesting no correlation between both proxies, whereas in males PC2 (eigenvalue = 25.7%) is almost exclusively represented by a gradient of hematocrit.

## Discussion

In the colony of Cory's shearwaters breeding at Berlengas, behaviour during the pre-laying period is highly dependent on the sex of the individual. Previous studies at this site had already shown that attendance cycles during the pre-laying period were a

lot higher in males than in females (Granadeiro et al., 1998b; Jouanin et al., 2001) supporting the nest guarding hypothesis. Yet, no study has previously shown how these differences in behaviour are expressed at-sea for both sexes. In concordance with the attendance cycles reported by Granadeiro et al. (1998a) and Jouanin et al. (2001), trip durations were a lot shorter and size of foraging areas a lot smaller for males than for females suggesting that males feed closer to the colony since staying away from the nest for longer periods could result in the nest being occupied by new individuals or close neighbours (Brooke, 1990; Mougín, 2000; Mougín et al., 2002).

Currently, approximately 130 nests can be counted in the study colony at Berlengas Island, from which 90 are frequently monitored each year for breeding success. These nests showed to vary in a gradient of many variables. For instance, nests with a higher amount of small rocks as substrate are more successful than nests with a soil substrate (Figure 5). Although this may seem contradictory, small rocks could represent a better drainage material than soil and/or rocks. In fact, as a rule to avoid flooding events in artificial chambers used in zoos for penguins of the genus *Spheniscus*, it is highly recommended the use of sand, pebbles or natural rocks as long as a kind of drainage exists (Penguin-TAG, 2001). Our results also indicate that a smaller nest entrance is associated to better quality nests. Smaller entrances may keep temperatures more constant inside the chamber, avoiding also a direct insulation that could lead to the loss of the egg due to heat stress as observed in Magellanic Penguins *Spheniscus magellanicus* (Stokes and Boersma, 1991). Moreover, small entrances have the extra advantage of being easier to defend. This agrees to some extent to the results found by Pearson et al (2005) in common terns *Sterna hirundo*, where older birds were better at defending their nests leading to a higher breeding success. Our results also show that smaller nest entrances are commonly related to smaller chambers leading also

to an increase in the quality of the nest. Smaller chambers have shown to have a better air circulation, which could compensate a greater exposition of the nest towards the sun (Penguin-TAG, 2001). In fact, in Vila Islet, Azores, Ramos et al (1997) showed that Cory's shearwater nesting in wider nest cavities had lower hatching success. However, the chamber size should at least allow both individuals to sit inside the nest one next to the other; if not, birds will try to enlarge the chamber by further excavating (Ramos et al., 1997).

Nest characteristics play an important role in the breeding success of many seabird species (e.g. in common guillemots *Uria algae* (Harris et al., 1997; Kokko et al., 2004), Humboldt penguins *Spheniscus humboldti* (Paredes and Zavalaga, 2001), shags *Phalacrocorax aristotelis* (Potts et al., 1980), Manx shearwater (Thompson, 1987)). Whether this determines nest-site fidelity appears to vary among different species. For example, Thompson (1987) tested the flooding likelihood of Manx shearwater nests based on the slope of the ground and depth of the nest. Yet, despite showing that nests that are less prone to be flooded have a higher breeding success, birds would not move into better quality nests. On the other hand, in species like common guillemots (Harris et al., 1997) and shags (Potts et al., 1980) changes to nests of better qualities have been reported. Furthermore, common guillemot individuals that lost a better quality nest would rather remain as “floaters” near their previous breeding site for many years without breeding before moving into a lower quality nest to breed (Kokko et al., 2004). Cory's shearwater, are known to have high nest fidelity (Mougin et al., 2002; Thibault, 1994) – although not absolute – and that increasing breeding experience will increase mate and nest-site fidelity (Mougin, 2000). This may partially explain why females of high quality nests showed to forage closer to the colony in this study, suggesting that females could be helping males in nest guarding duties. In concordance, these high-

quality-nest females might be more efficient foragers since staying close to the colony would imply directly competing with males foraging in the same area as inferred by Cairns (1989), Elliott et al (2009) and Lewis et al (2001) when linking the size of colonies to ocean productivity. Moreover, poor nest quality was also related to males performing longer foraging trips and exploring larger foraging areas suggesting a poor guarding behaviour or a lack of interest in that specific nest. Indeed, males' behaviour seems to be strongly related to single nest features such as size entrance and how close neighbour nests are located. In fact, the size of the nest entrance is positively correlated to the area male individuals explore for foraging which supports the previous results that males will rather prefer to guard nests with small entrances (better quality nests). On the other hand, the percentage of flying (searching) time in males is reduced when having closer neighbours which at the same time increases the areas explored for foraging. In a very broad way, this may support the information centres theory of Ward and Zahavi (1973), yet more detailed analyses should be done to confirm this.

Females on the contrary do not appear to show a clear pattern in their behaviour, and individual nest features seem to equally be related to variables in short or long trips. Hence it could be assumed that females' behavioural patterns at-sea are independent of specific nest features during the pre-laying period. Furthermore, assessing the individual quality differences during the pre-laying period in females is difficult when using the quality proxies. Males on the other hand, show a clear tendency in which age highly correlates with weight of the individual and to some extent to the breeding success observed in previous years. Moreover, the distribution pattern of males (represented by the number of nest they occupy) along the PC1 gradient of males' quality (Figure 6) follows a similar pattern to the nest distribution along the PC1 gradient for nest quality (Figure 5). This suggests that higher quality males are related to higher quality nests

increasing the probability of breeding success (Sæther et al., 1997). Breeding experience is commonly used as a proxy of individuals' quality as it has been shown that only a small proportion of natural populations actually contribute to future generations (Newton, 1995) implying that breeding experience increases breeding success (Cézilly and Nager, 1996; Moreno, 2003). Nevertheless, Sæther et al. (1997) suggested that it is the balance between parents' quality and environmental variables what ultimately determines breeding success. Individual breeding success has also been associated to the age of the individual (Sæther, 1990) and further to foraging skills (Greig et al., 1983; Porter and Sealy, 1982).

Other proxies commonly used to assess individual quality are weight of individuals (body mass) and hematocrit values. Low hematocrit is usually associated to anaemia due to parasites or other chronic diseases in birds, while a high hematocrit could be an indicator of dehydration (Amat et al., 2009) or aerobic stress (Carpenter, 1975). Nonetheless, weight and hematocrit are highly variable and change over time (Hatch and Smith, 2010). Hematocrits for instance, may change according to the sex and age of the individual, day, levels of stress, etc. (Fair et al., 2007). This may partially explain why hematocrit did not correlate to any other quality proxy in this study despite sampling was uniform in terms of time of the day and bird manipulation for all individuals and within a short period of time (less than a week). In a similar way, body mass (weight) tends to vary with fluctuations in the environmental conditions (Rintamäki et al., 2009), and may be highly dependent on the foraging success short before capture.

In summary, a clear difference in at-sea behavioural patterns expressed by males and females is observed in the pre-laying period. Females forage at a larger spatial scale than males whose spatial and temporal foraging scale seems to be constrained by the

fact that they have to guard the nest against conspecifics during this period. Furthermore, some of the at-sea behaviours in males such as the size of the area explored for foraging and the trip duration appear to be sensitive to changes in the variables determining nest quality such as the size of the nesting chamber and nest entrance. This leads to the final conclusion that the quality of the male is crucial to the subsequent pairs' breeding success, as most of the outcomes in that breeding season may depend on the correct behaviour and achievements each male will obtain during the pre-laying period.

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## **CHAPTER 2**

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## THE FORAGING PATTERNS OF CORY'S SHEARWATER IN THE PRE-LAYING PERIOD AS A RESULT OF OCEANOGRAPHIC FEATURES AT DIFFERENT SPATIAL RESOLUTIONS

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### **Introduction**

Foraging patterns in Cory's shearwater *Calonectris diomedea* and other seabirds have been widely described especially during the chick rearing period e.g. (Baduini and Hyerenbach, 2003; Granadeiro et al., 1998a; Granadeiro et al., 1998b; Granadeiro et al., 1998c; Guilford et al., 2008; Magalhaes et al., 2008; Navarro and Gonzalez-Solis, 2009; Navarro et al., 2007; Navarro et al., 2009b; Phillips et al., 2009; Ramos et al., 2009; Weimerskirch et al., 1997; Weimerskirch et al., 1994). Along this period and during incubation, procellariiforms often opt for a dual-foraging strategy if resource availability is heterogeneous around the breeding areas (Paiva et al., 2010; Phillips et al., 2009) and an unimodal strategy if the colony is located close to high productive areas (Baduini and Hyerenbach, 2003; Granadeiro et al., 1998c; Navarro and Gonzáles-Solis, 2009). A dual foraging strategy implies alternating short and long foraging trips (Chaurand and Weimerskirch, 1994). Short trips are often associated to be at the expenses of the adult's body reserves but energetically beneficial for chicks whereas long trips are commonly associated with an improvement of adults body condition (Granadeiro et al., 1998c; Weimerskirch, 1998; Weimerskirch et al., 1997; Weimerskirch et al., 1994). This suggests that the



chick represents a temporal and spatial constrain to the foraging strategy of parents. In fact, studies of the diet of breeding adult individuals showed a similar feeding ecology in both sexes in Cory's shearwater in terms of geographic area and prey ingestion (Navarro et al., 2009a). Similar results were obtained by Ramos et al., (2009) during the incubation period for the same species which could be related to the fact that during both periods the role of both parents are alike. During the pre-laying period however, these roles are very different for each sex. Thus, while males engage in nest competition and defence from conspecifics (Ramos et al., 1997), females support the energy costs of egg production (Jouanin et al., 2001). This role segregation between individuals is reflected on the behavioural patterns at sea (see chapter 1). Yet, if these behavioural patterns are influenced by oceanic features such as productivity proxies (i.e. Chlorophyll-a [Chla] concentrations and Sea Surface Temperatures [SST]) and depth is still unknown.

Several studies have shown that the foraging locations of seabirds are significantly associated with elevated chlorophyll concentrations in the ocean (e.g. Gremillet et al., 2004; Louzao et al., 2006; Magalhaes et al., 2008; Navarro and Gonzalez-Solis., 2009; Yen et al., 2006). Yet, as top predators, seabirds feed at 2 or 3 trophic levels higher in the food chain. In consequence, correlating seabird distribution and indices of primary production such as Chl-a concentration and SST can be misleading as it can overlook mismatches in intermediate trophic levels (Gremillet et al., 2008). The match-mismatch hypothesis (Cushing, 1974) refers to discrepancies in the distribution of prey and predator along a temporal scale occurring at usually 2 lower trophic levels such as phytoplankton and fishes. Yet, when including more levels into the trophic chain top and bottom extremes of the food web seem to match again in distribution (e.g. Gremillet et al., 2004; Gremillet et al., 2008).

The use of remote sensing techniques to collect environmental data (i.e. chl-a and SST) has been increasing exponentially since the last decade (reviewed by Tremblay et al., 2009). However, the great majority of studies relating these data to marine predator distributions employ free access grids from satellites like MODIS – Aqua, MODIS - Terra and SeaWiFS (but see Gremillet et al., 2004; Gremillet et al., 2008; Kai et al., 2009). These grids are freely available at spatial resolutions of 9-km and 4-km (hereafter referred to as *grid* resolutions) and at temporal scales varying from days to months. Conversely, bird satellite tracking devices have been improving in miniaturization and accuracy (see reviews by Burger and Shaffer, 2008; Wilson et al., 2002) for characteristics of the different tracking systems). Therefore the spatial and temporal resolution of remote sensing products employed in a study using high resolution tracking devices could be generating a considerable loss of information, hence influencing the interpretation of data obtained by such devices. The acquirement of environmental products at greater grid resolutions on the other hand requires additional processing starting from lower level products (Figure 7) and is often very time consuming.

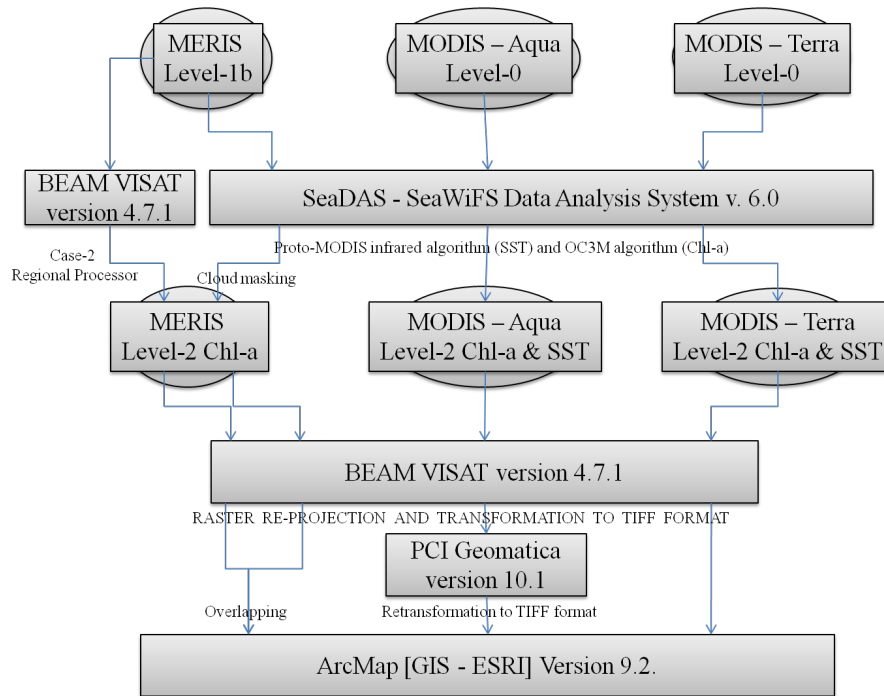


Figure 7. Flux diagram indicating the processing steps to obtain the Level-2 products used to assess the foraging behaviour of Cory's shearwater.

In this study remote sensing environmental data was obtained at a

- (i) 9-km grid size for Chl-a and SST from MODIS-Aqua at a monthly temporal scale;
- (ii) (ii) 0.25-km grid size for Chl-a and SST from MODIS-Aqua at a daily temporal scale; and
- (iii) 0.3-km grid size for Chl-a from MERIS at a daily temporal scale
- (iv) 1-km grid size for depth values from ETOPO1

aiming to assess (a) the influence of environmental variables on the foraging patterns of male and female Cory's shearwater at sea during the pre-laying period and; (b) the influence of remote sensing's grid and temporal resolution on the interpretation of such

results. It is expected that foraging patterns of males and females will differ, as their roles during this period are too different; and that the interpretation of such differences will vary with the grid and temporal resolutions of the employed remote sensing products, being a lot more accurate when using small grid sizes (high resolution images).

## **Methods**

### Study area and bird count

Berlengas is an archipelago formed by three groups of rocky islets (Berlenga, Estelas and Farilhões) and is surrounded by rich feeding grounds as a result of the combination of bathymetric features with wind and ocean circulation (Barton, 2001). These features enhance upwelling regimes which, nonetheless, have been weakening in the last 60 years especially in the warm season (April – September) (Lemos and Pires, 2004; Lemos and Sansó, 2006; Relvas et al., 2007).

This study was carried out on Berlenga Island (39.413611N, -9.508056E) between 10 April – 10 May 2010. Cory's shearwaters belonged to the colony situated on the eastern side of the "Old Island" of Berlenga (39.413937N, -9.504926E) where approximately 130 pairs nest. Most individuals of this colony are ringed and an age approximation is possible following EURING codes (Appendix 2). In addition, data of the reproductive success (presence of a chick) was obtained later that year (August) as a measure of individual quality that could account for differences within individuals.

### GPS tracking devices

At sea foraging behaviour was obtained with GPS tracking data (for a more detailed description refer to Chapter 1). CatTaq Travel Loggers (Perthold Engineering

LLC) were employed as GPS-loggers. The plastic case was removed and replaced by a 7cm long thermo-retractile rubber sleeve, which reduced the total weight to 17g (Figure 1, Chapter 1). Each GPS-logger was then attached to the back contour feathers of 18 males and 22 female individuals. The total weight of the GPS-logger represented between 1.6% and 2.6% of the birds weight which has been suggested to not have a negative effect on the instrumented seabird (Phillips et al., 2003). GPS-loggers recorded data (geographic position, altitude, ground speed, course, distance) in 5 minute intervals between 05h and 22h every day, time in which birds are more likely to be foraging at sea. Subsequently, trips were classified as short ( $\leq 1$  day duration) or long ( $\geq 2$  days duration) trips (see Chapter 1 for details).

#### Environmental data

Three environmental variables were employed to assess at-sea behaviours in Cory's shearwater: Chlorophyll-a concentration (Chl-a), Sea Surface Temperature (SST) and bathymetry. The remote sensing products to obtain these variables were taken by MERIS (Medium Resolution Imaging Spectrometer) on the Envisat platform from the European Spatial Agency (ESA) and MODIS (Moderate Resolution Imaging Spectroradiometer) on Terra (EOS AM<sup>1</sup>) and Aqua (EOS PM) platforms from the National Aeronautics and Space Administration (NASA). MERIS full resolution (260\*290m) Level-1b (Figure 8) products were collected and provided by Brockmann-Consult and GKSS (Gesellschaft zur Förderung der Kernenergie in Schiffbau und Schiffstechnik - Society for the Promotion of Nuclear Energy in Shipbuilding and Naval

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<sup>1</sup> EOS stands for Earth Observing System. AM meaning it has the mornings equatorial crossing time in case of the Terra satellite and PM the afternoons equatorial crossing time for Aqua satellite

Technology) through ESA's "Rolling Archive" while MODIS Level-0 products were obtained from the Ocean Colour Website from NASA ([www.gsfc.nasa.gov](http://www.gsfc.nasa.gov)).

In addition, a low resolution (9-km) MODIS Level-2 monthly average product corresponding to the study period for Chl-a concentrations and SST was obtained from <http://oceancolor.gsfc.nasa.gov/>.

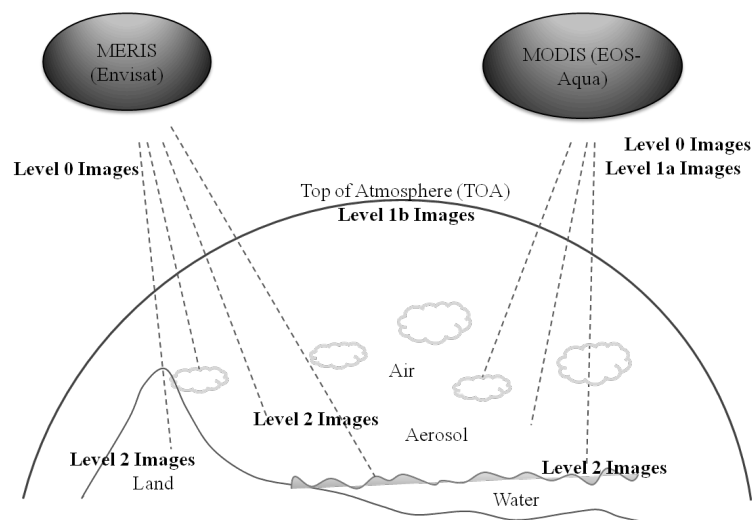


Figure 8. MERIS and MODIS image Level equivalents and product contents. Level 1 images are calibrated at TOA radiance and contain geolocated data. Yet atmospheric corrections need to be made to obtain geophysical measurements (Level 2)

The high amount of cloud cover present in MERIS and MODIS products during the study period encouraged the use of images taken at different times of the day, hence the use of different satellites to fill in the gaps. The limitations for data comparison due to the difference in orbits, as well as in the processing algorithms, were solved by creating a linear function on the base of recorded points at open ocean (away of the influence of river discharges or coastline effects) in overlapping images taken on the

same day (figure 9). This way, each MERIS value was transformed into its equivalent in MODIS values.

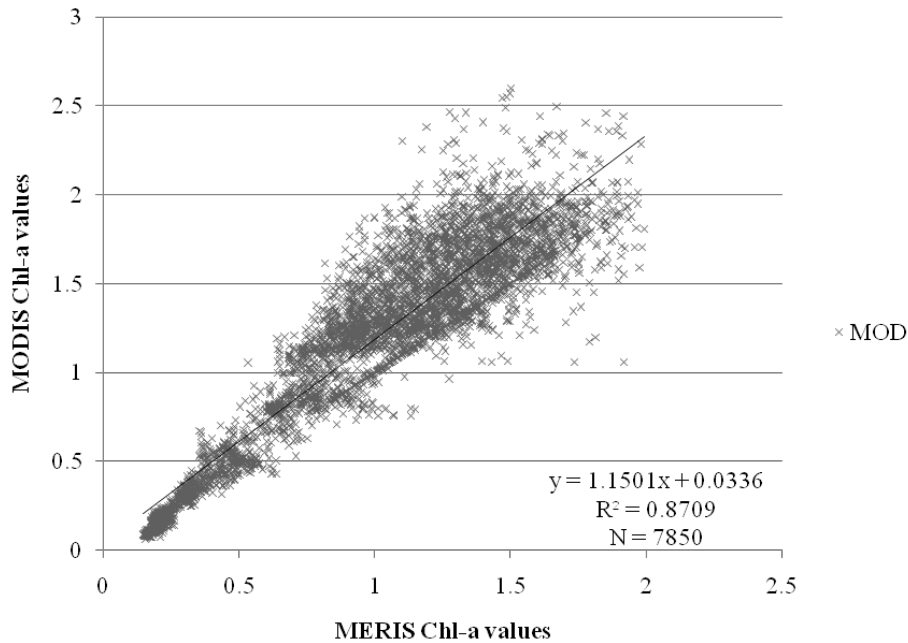


Figure 9. Linear function relating Chlorophyll data from MODIS and MERIS instruments

Bathymetry data on the other hand were obtained from NOAA's National Geophysical Data Centre ETOPO1 provided by the Mediterranean Science Commission (<http://www.ngdc.noaa.gov/mgg/global/global.html>) at a 1-km spatial resolution grid.

### Image Processing

The processing of remote sensing images was performed in collaboration with the Departamento de Ciências da Terra da Universidade de Coimbra with Vasco Mantas and Dr. Alcides Pereira. MODIS Level-0 products were processed to Level-2 products using SeaDAS - SeaWiFS Data Analysis System v. 6.0, which allowed obtaining

products with a resolution of 250\*250m. MERIS Level-1b products were processed to Level-2 products using the Case-2 Regional Processor (BEAM) processor (Doerffer R. and H. Schiller (2008): MERIS Regional Coastal and Lake Case 2 Water Project - Atmospheric Correction ATBD, GKSS Research Center 21502 Geesthacht Version 1.0 18. May 2008). However, SeaDAS - SeaWiFS Data Analysis System v. 6.0 was employed to mask the clouds on MERIS images as the algorithm to flag clouds in BEAM's processor is still under development (R. Doerffer pers. comm.). The resulting Level-2 products from MODIS (Chl-a and SST) and MERIS (Chl-a) were re-projected using BEAM/VISAT version 4.7.1 and the subsets corresponding to Chl-a and SST were exported in a GeoTIFF format (Figure 7).

The final Level-2 products employed in this study included: (i) almost daily (N = 22) MERIS Chl-a concentration products at a 0.3-km spatial resolution; (ii) MODIS Chl-a (N = 11) concentration and SST (N = 11) products at a 0.25-km; (iii) a monthly averaged 9-km spatial resolution MODIS product for Chl-a concentrations and SST values; and (iv) a 1-km spatial resolution bathymetric product.

## Data Analysis

### Path sinuosity estimation

The path sinuosity index at each recorded flying point was represented by the ratio of straight-line distance between two points (real distance) relative to the potential maximum distance the bird could have travelled (calculated using the instant speed recorded at that specific point – theoretical distance) (adapted from Weimerskirch et al., 2002). An index equivalent or higher than three was considered a sinuous trip (adapted from Grémillet et al., 2004).



## Home Range estimators

Three home range scales (hereafter referred to as *spatial* scale) were employed for different purposes: (i) The Minimum Convex Polygon<sup>1</sup> (MCP) to represent a general characterization of the available habitat for each individual, and two approaches of Kernel Density Estimators<sup>2</sup> (KDE): (ii) 50% Sea-point kernels (hereafter called S50K), which represented the areas at-sea of real interest within the respective MCP (i.e. where the bird flies, rests, feeds), and (iii) 50% foraging-point kernels (hereafter named F50K) which exclusively represented the areas where birds were engaged in foraging activities (determined by trip sinuosity indexes higher or equal to three). These estimators were calculated with the Animal Movement extension 2.0 (Hooge and Eichenlaub 1997) using exclusively flying points (point recorded speed  $\geq 9$ km/h, see chapter 1 for details and/or Guilford et al., 2008). For each estimator, trips were segregated by duration (short trips = 1 day long, long trips  $\geq$  days duration) – see chapter 1. Furthermore, 50% FKD estimates were chosen to represent the core areas of feeding activity following previous studies (e.g. Hamer et al. 2007).

## Data extraction

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1 The Minimum Convex Polygon (MCP), also known as the Minimum Area polygon Method (MAM, Mohr C.O. (1947) Table of equivalent populations of North American mammals. American Midland Naturalist 37) is a non-probabilistic method in which a convex polygon is constructed by connecting the outer locations (x,y coordinate system). Yet, it “fails” when some part of the true shape of the home range is concave.

2 The kernel is a nonparametric, scaled down probability density function, which calculates home range boundaries based on the utilization distribution (UD, Worton B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.)

To obtain the highest amount of environmental data in short trips, Chl-a concentrations and SST values for each pixel contained at different spatial scales (MCPs and kernels) were extracted from the satellite (MERIS and/or MODIS) product corresponding to the same date if available. If no image was available for that day or if data overlapped with pixels corresponding to clouds, data for those pixels were obtained averaging the correspondent pixel value of the day immediately after and before (if both were available). Otherwise data were equivalent to the value of either the closest day before or after. In addition Chl-a concentration data and SST values were also extracted for each polygon from the 9-km MODIS monthly grid and depth values from the ETOPO1 product.

To calculate the values in long trips, each fine grid resolution satellite image was transformed into a point grid and values for each day were extracted to all spatial scales (MCP, Sea-point kernels and foraging kernels) and a mean obtained. This way temporal resolution was controlled for the analysis of long trips, each value becoming an equivalent to a monthly average (i.e. comparable with the 9-km MODIS monthly grid) but at a finer grid resolution.

## Statistics

All environmental data was log transformed to approximate normality. Two approaches were then employed to assess differences in the habitat use at different scales of males and females and within males. Data were processed in R version 2.11.1 (<http://www.R-project.org>):

1. Environmental data were processed with Linear Mixed Models (LMM) fit by REML (Restricted Maximum Likelihood) using the “nlme” library (Pinheiro et

al., 2009). These models were used as they account for pseudo-replication (dependency) among variables. Following model was applied:

- between males and females

$$model \leftarrow lme(y \sim x, random = \sim 1 \mid ring)$$

where: x = male/female;

y = see table below (VI) for long and short trips

**Table VI.** List of variables represented by "y" for the application of Linear Mixed Models. MCP = Minimum Convex Polygon. See text for further explanation of variables.

		"y" value			"y" value
9- km	SST	MCP	0.3- km	SST	MCP
		Sea-point kernels 50%			Sea-point kernels 50%
		Foraging-point kernels 50%			Foraging-point kernels 50%
	Chl-a	MCP		Chl-a	MCP
		Sea-point kernels 50%			Sea-point kernels 50%
		Foraging-point kernels 50%			Foraging-point kernels 50%
	Bathymetry	MCP		Bathymetry	MCP
		Sea-point kernels 50%			Sea-point kernels 50%
		Foraging-point kernels 50%			Foraging-point kernels 50%

- and within males:

x = successful/unsuccessful breeders (with chick/without chick);

x = young/old individuals (young ≤ 10 years; old ≥ 11 years);

y = same as above (Table VI)

Only males were considered in this analysis because they show clear behavioural patterns during the pre-laying period than females. In addition, it is the quality of the male that seems to determine the subsequent breeding success of the pair (see chapter 1 for details).

1. Environmental data was also assessed using a Multivariate Analysis of Variance (MANOVA). Although this test does not account for dependency in the dataset, the use of kernels reduce the dependency effect (Worton B. J., 1989). Following function was applied:

$$model <- manova(y\sim x)$$

where x = male/female; and “y” binds together three separate response variables: MCPs, foraging-point and sea-point kernels into one single multivariate response variable

## **Results**

A total of 236 trips were recorded for 33 individuals (17 males and 16 females). Out of these, 198 trips were short trips and 38 long trips.

### *Linear Mixed Models*

#### Long Trips

At a monthly temporal scale and a grid resolution of 9-km, males performing long trips used areas with significantly higher Chl-a concentrations (more productive areas) than females performing long trips in all spatial scales (LMM for MCP:  $F_{1,22} = 9.38175$ ,  $P = 0.0057$ ; LMM for S50K:  $F_{1,22} = 4.59368$ ,  $P = 0.0434$  and LMM for F50K:

$F_{1,22} = 8.75492$ ,  $P = 0.0072$ ) (Table VII). However, no significant differences were encountered within the spatial scales in terms of Chl-a concentrations. Males and females home range areas also showed no significant difference in SST values during long trips. Neither was there a significant difference among spatial scales.

At a grid resolution of 0.3-km, males performing long trips also exploited areas with significantly higher values of Chl-a than females did when performing long trips at all spatial scales (LMM for MCP:  $F_{1,22} = 4.74554$ ,  $P = 0.0404$ ; LMM for S50K:  $F_{1,22} = 7.45464$ ,  $P = 0.0122$  and LMM for F50K:  $F_{1,22} = 6.077927$ ,  $P = 0.022$ ) (Table VII). Yet, post-hoc t-tests showed that only in females a significant difference among MCPs and F50K exists (LMM for Females<sub>MCP and F50K</sub>:  $F_{2,61} = 8.3558$ ,  $P = 0.0006$ ).

Table VII. Results of the Linear Mixed Models (LMM) fit by REML testing the differences between males and females in terms of environmental variables during long foraging trips. F= females, M = Males, SST = Sea Surface Temperatures, Chl-a = Chlorophyll-a concentrations, MCP = Minimum Convex Polygon, S50K = 50% sea-point kernel, F50K = 50% foraging-point kernel. **Bold** denotes significant results.

9KM									
SEX	SST			Chl-a			DEPTH		
	MCP±SD	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD
F	16.16 ± 0.37	16.30 ± 0.47	16.29 ± 0.53	0.40 ± 0.12	0.39 ± 0.28	0.31 ± 0.18	-668 ± 1421	-3331 ± 1531	-3740 ± 1127
M	16.12 ± 0.31	16.28 ± 0.60	16.28 ± 0.60	0.66 ± 0.31	0.66 ± 0.33	0.65 ± 0.39	-1400 ± 1361	-1748 ± 1680	-1986 ± 1925
F <sub>DF1,22</sub>	0.06	0.02	0.01	9.38	4.59	8.76	1.31	6.71	10.89
P	0.8049	0.8968	0.9259	<b>0.0057</b>	<b>0.0434</b>	<b>0.0072</b>	0.2647	<b>0.0167</b>	<b>0.0033</b>
0.3KM									
SEX	SST			Chl-a			DEPTH		
	MCP	S50K	F50K	MCP±SD	S50K±SD	F50K±SD	MCP	S50K	F50K
F				0.89 ± 0.20	0.64 ± 0.45	0.47 ± 0.54			
M				1.28 ± 0.66	1.13 ± 0.55	1.10 ± 0.79			
F <sub>DF1,22</sub>				4.75	7.45	6.08			
P				<b>0.0404</b>	<b>0.0122</b>	<b>0.022</b>			

Table VIII. Results of the Linear Mixed Models (LMM) fit by REML testing the differences between males and females in terms of environmental variables during short foraging trips. F= females, M = Males, SST = Sea Surface Temperatures, Chl-a = Chlorophyll-a concentrations, MCP = Minimum Convex Polygon, S50K = 50% sea-point kernel, F50K = 50% foraging-point kernel. **Bold** denotes significant results.

9KM									
SEX	SST			Chl-a			DEPTH		
	MCP±SD	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD
F	16.02 ± 0.09	15.98 ± 0.15	16.00 ± 0.17	0.86 ± 0.43	0.92 ± 0.23	0.72 ± 0.28	-590 ± 1143	-133 ± 452	-151 ± 356
M	16.05 ± 0.10	16.06 ± 0.14	16.02 ± 0.12	1.01 ± 0.38	1.06 ± 0.29	1.07 ± 0.21	-615 ± 1218	-75 ± 154	-79 ± 175
F <sub>value</sub>	2.8	5.64	1.0377	7.6989	5.253	3.364	0.02	1.08	3.38
P	0.09	<b>0.0019</b>	0.311	<b>0.0061</b>	<b>0.0238</b>	0.06987	0.9006	0.3079	0.06754
DF	1,57			1,57			1,57		
0.3KM									
SEX	SST			Chl-a			DEPTH		
	MCP± SD	S50K± SD	F50K± SD	MCP± SD	S50K±SD	F50K±SD	MCP	S50K	F50K
F	15.58 ± 2.10	15.43 ± 2.39	15.90 ± 1.99	0.88 ± 0.75	0.98 ± 0.90	0.84 ± 0.78			
M	14.84 ± 2.25	14.74 ± 2.30	14.99 ± 2.38	1.04 ± 1.61	1.35 ± 1.51	1.26 ± 1.55			
F <sub>value</sub>	2.51	1.90	3.09	1.39	1.13	0.31			
P	0.1152	0.1709	0.0813	0.2413	0.2909	0.5781			
DF	1,106			1,65					

Table IX. Results of the Multivariate Analysis of variance (MANOVA) testing the differences between males and females in terms of environmental variables during long foraging trips. F= females, M = Males, SST = Sea Surface Temperatures, CHL-A = Chlorophyll-a concentrations, MCP = Minimum Convex Polygon, S50K = 50% sea-point kernel, F50K = 50% foraging-point kernel. **Bold** denotes significant results.

9KM									
SEX	SST			Chl-a			DEPTH		
	F <sub>DF1,34</sub> =0.057, P=0.98			F <sub>DF1,34</sub> =4.79, P<0.001			F <sub>DF1,34</sub> =4.46, P<0.01		
	MCP±SD	S50K±SD	F50K±SD	MC±SDP	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD
F	16.16 ± 0.37	16.30 ± 0.47	16.29 ± 0.53	0.40 ± 0.12	0.39 ± 0.28	0.31 ± 0.18	-668 ± 1421	-3331 ± 1531	-3740 ± 1127
M	16.12 ± 0.31	16.28 ± 0.60	16.28 ± 0.60	0.66 ± 0.31	0.66 ± 0.33	0.65 ± 0.39	-1400 ± 1361	-1748 ± 1680	-1986 ± 1924
F <sub>DF1,36</sub>	0.08	0.02	0.01	13.59	6.96	13.68	1.63	8.28	12.54
P	0.7766	0.9	0.931	<b>0.0007</b>	<b>0.0122</b>	<b>0.0007</b>	0.2097	<b>0.0067</b>	<b>0.0011</b>
0.3KM									
SEX	SST			Chl-a			DEPTH		
	F <sub>DF1,34</sub> =3.43, P=0.03			F <sub>DF1,34</sub> =3.43, P=0.03			F <sub>DF1,34</sub> =3.43, P=0.03		
	MCP	S50K	F50K	MCP	S50K	F50K	MCP	S50K	F50K
F				0.89 ± 0.20	0.64 ± 0.45	0.47 ± 0.54			
M				1.28 ± 0.66	1.13 ± 0.55	1.10 ± 0.79			
F <sub>DF1,36</sub>				7.83	8.76	8.18			
P				<b>0.0082</b>	<b>0.0054</b>	<b>0.0070</b>			



Table X. Results of the Multivariate Analysis of variance (MANOVA) testing the differences between males and females in terms of environmental variables during short foraging trips. F= females, M = Males, SST = Sea Surface Temperatures, Chl-a = Chlorophyll-a concentrations, MCP = Minimum Convex Polygon, S50K = 50% sea-point kernel, F50K = 50% foraging-point kernel. **Bold** denotes significant results.

		9KM								
SEX	SST			Chl-a			DEPTH			
	<b>F<sub>DF3,59</sub>=6.0261, P=0.0012</b>			<b>F<sub>DF3,59</sub>=3.53, P=0.0201</b>			F <sub>DF3,186</sub> =0.83, P=0.4807			
	MCP±SD	S50K±SD	F50K±SD	MC±SDP	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD	
F	16.02 ± 0.09	15.98 ± 0.15	16.00 ± 0.17	0.86 ± 0.43	0.92 ± 0.23	0.72 ± 0.28	-590 ± 1143	-133 ± 452	-151 ± 356	
M	16.05 ± 0.10	16.06 ± 0.14	16.02 ± 0.12	1.01 ± 0.38	1.06 ± 0.29	1.07 ± 0.21	-615 ± 1218	-75 ± 154	-79 ± 175	
F <sub>value</sub>	4.33	18.40	3.58	3.49	4.50	10.51	0.03	1.77	2.50	
P	<b>0.04173</b>	<b>&lt;0.0001</b>	<b>0.0632</b>	0.06658	<b>0.03780</b>	<b>0.0019</b>	0.8595	0.1848	0.1152	
DF	1,61			1,61			1,188			
		0.3KM								
SEX	SST			Chl-a			DEPTH			
	F <sub>DF3,110</sub> =1.02, P=0.386			F <sub>DF3,71</sub> =1.81, P=0.1538						
	MCP±SD	S50K±SD	F50K±SD	MC±SDP	S50K±SD	F50K±SD	MCP±SD	S50K±SD	F50K±SD	
F	15.58 ± 2.10	15.43 ± 2.39	15.90 ± 1.99	0.88 ± 0.75	0.98 ± 0.90	0.84 ± 0.78				
M	14.84 ± 2.25	14.74 ± 2.30	14.99 ± 2.38	1.04 ± 1.61	1.35 ± 1.51	1.26 ± 1.55				
F <sub>value</sub>	2.42	1.34	2.58	0.28	1.64	1.36				
P	0.1230	0.2486	0.1109	0.6013	0.2044	0.2470				
DF	1,112			1,73						

Females also foraged at significantly deeper waters than males at the smaller spatial scales (LMM for S50K:  $F_{1,22} = 6.7127$ ,  $P = 0.0167$  and LMM for F50K:  $F_{1,22} = 10.89239$ ,  $P = 0.0033$ ) (Table VII and figure 10).

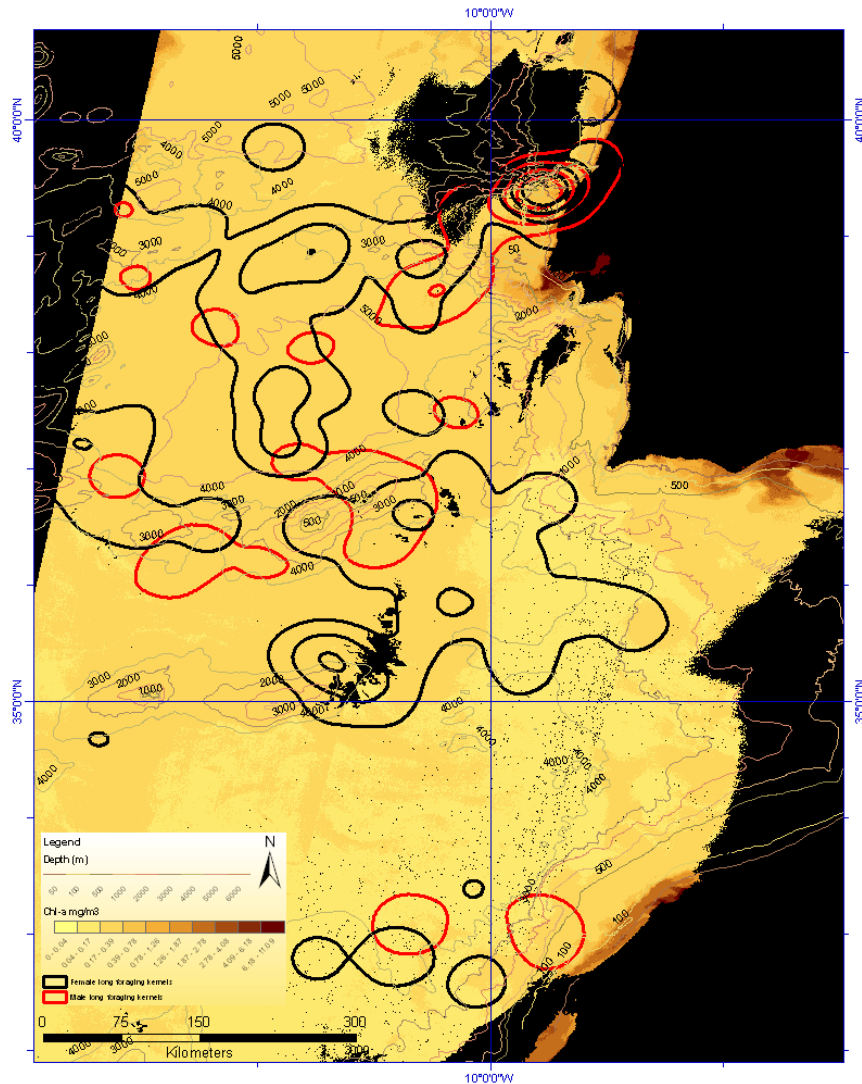


Figure 10. Ocean productivity (Chl-a) for the 26th of April 2010 showing all foraging kernels identified for long trips of males (red) and females (black). Kernel smoothing factor 20000m. . Black areas are equivalent to no-data (i.e. sun glint, clouds and continent) Image obtained from MERIS products. Grid resolution 300m. Female foraging trips extend further west, but satellite swatch did not reach that area. Contours for bathymetry are also shown

Furthermore, post-hoc t-tests performed between different spatial scales revealed that depth values of MCPs differed significantly from depth values of 50% sea-point and foraging kernels in males and in females (LMM for Males<sub>MCP and kernels</sub>:  $F_{2,25} = 11.245$ ,  $P = 0.0003$ ; LMM for Females<sub>MCP and kernels</sub>:  $F_{2,61} = 44.436$ ,  $P < 0.0001$ ).

### Short trips

At a monthly temporal scale and a grid resolution of 9-km, results show that males exploited more productive areas (higher concentrations of Chl-a) than females did at a MCP and S50K spatial scale (LMM for MCP:  $F_{1,57} = 7.6989$ ,  $P = 0.006133$  and LMM for S50K:  $F_{1,57} = 5.253$ ,  $P = 0.0238$ ) (Table VIII). However, no significant differences were found between spatial scales for males or for females. The analysis of SST values at different spatial scales nonetheless showed significant differences between males and females only at S50K (LMM for S50K:  $F_{1,57} = 5.6441$ ,  $P = 0.0192$ ) (Table VIII). However, no significant differences were observed between different spatial scales for males or for females.

At a daily temporal scale and a grid resolution of 0.3-km, no significant differences were observed between males and females in terms of Chl-a concentrations or SST values (Table VIII). In fact, the spatial scale also did not differ among these environmental variables in males nor females. Likewise, males and females did not differ in the use of bathymetric features at different spatial scales (Table VIII).

Yet, post-hoc t-test at different spatial scales showed that MCP differ significantly from 50% sea-point and foraging-point kernels in males and in females (LMM for Males<sub>MCP and kernels</sub>:  $F_{2,44} = 27.87$ ,  $P < 0.0001$ ; LMM for Females<sub>MCP and kernels</sub>:  $F_{2,76} = 5.69$ ,  $P = 0.0042$ ).

An overall preference of Cory's shearwater to forage in areas slightly less productive than the areas containing the highest productivity levels within their home range was observed in short and long trips for males and females. This trend was enhanced when the analysis was performed at higher resolution grids (Tables VII and VIII). Last but not least, the analyses of differences between individuals of different ages and previous breeding success only revealed that at a large grid resolution young males used MCPs with significantly higher SST values than old individuals (younger males ( $16.9 \pm 0.4$ ) vs. old males ( $15.1 \pm 0.5$ ); LMM:  $F_{1,95} = 8.0313$ ,  $P = 0.0053$ ).

#### *Multiple Analyses Of Variance (MANOVA)*

The results obtained by analyzing the environmental data using a MANOVA confirmed the results obtained by applying LMM for long and short trips at different temporal and spatial scales at different grids (Tables IX and X).

## **Discussion**

### Cory's shearwater behaviour

Results show that males are foraging at significantly higher productive areas than females are during short and long trips. This not only confirms trophic segregation during the pre-laying period due to a difference in roles but also suggests that females could be searching for specific nutrients, hence specific prey to support the cost of egg production. For instance, a considerable shift in the diet of little terns (*Sterna albifrons*) towards insects was observed during the egg production period to obtain proteins (Cattray et al., 2006). On the other hand, the use of nitrogen ( $^{15}\text{N}$ ) stable isotopes showed that during the pre-laying period Cory's shearwaters (no sexual segregation found) breeding on the Canary Islands fed at lower trophic levels than during the rest of the breeding

season (Navarro et al., 2007). Yet, Bearhop et al (2006) found that in several diving seabird species males feed at higher trophic levels than females during the chick rearing period.

Independently of the differences in area productivity between male and females, both showed a trend to not use the highest productive areas within their correspondent home ranges, although the differences between the spatial scales were not significant. For instance, in both sexes MCPs were areas with lower Chl-a concentrations. Within these areas, males and females select the most productive areas (S50K). However, within sea-point kernels they foraging activities (F50K) concentrate at slightly lower productive areas. This trend better supports the spatial match-mismatch theory (Cushing, 1974; Gremillet et al., 2008) at a coarse grid scale (9-km). The match-mismatch hypothesis suggests that the lowest trophic levels in a marine environment can match in distribution with the highest trophic levels (top predators) while mismatching with intermediate trophic levels. Such temporal match and mismatches occur because top predators are not feeding directly on Chl-a or SST but at some of the intermediate levels in the trophic chain. Gremillet et al. (2004, 2008) showed that despite mismatches in intermediate trophic levels, top predators distribution matched phytoplankton distribution. Conversely, our results indicate that potential mismatches can still be encountered between phytoplankton and top-predators, especially if studies are performed at a much finer grid resolution (Gremillet et al. (2004, 2008) grid size =1-km, temporal resolution = daily).

The areas at different spatial scales used by males and females also did not differ in terms of SST values during long trips. This could be attributed to the temporal scale employed in this analysis (monthly average values). In fact that data collection were distributed continuously along a period of the year in which the SST for the Portuguese

coastal upwelling zones in coastal and offshore regions oceans increases in an exponential form (Lemos and Pires, 2004). In the analysis of short trips, the 9-km resolution grid showed that males were interested in areas with SST values significantly higher than females whereas 0.3-km grids showed that such differences were not significant. The significant differences found at a 9-km grid during short trips could be explained in other species such as Gentoo penguins (*Pygoscelis papua*), macaroni penguin (*Eudyptes chrysolophus*), South Georgian shag (*Phalacrocorax (atriceps) georgianus*) and the Kerguelen shag (*P. (atriceps) verrucosus*) where males are able to dive deeper than females due to larger size (Bearhop et al., 2006). Yet in surface feeders such as Cory shearwaters only subtle differences may exist in the diving behaviour of males and females (Ramos et al., 2009). This is supported by the analysis of bathymetric features in which the areas exploited by males and females did not differ during short trips. Moreover, in spatial terms the areas used by both sexes during short trips almost completely overlapped, supporting the results obtained at finer grid resolutions. Yet, further analysis should be performed grouping short trips along the study period in a temporal scale to verify whether the continuous sampling may have biased such results.

During long trips however, females showed to be interested (S50K and F50K) at significantly deeper waters than males did, although the overall area used by both did not differ significantly in terms of depth. Females with interest areas located in deeper waters can be the result of females travelling significantly further away to open waters than males (see chapter 1) as early suspected by Granadeiro et al (1998a); Jouanin et al (2001). Although no significant differences were observed between the depth of areas used by males and females, there seems to be a trend of the latter to wander over deeper waters during long and short trips. Yet, it is clear that although both sexes explore vast

areas (MCPs), those of real interest (S50K and F50K) are significantly shallower within their home range and are probably related to specific bathymetric characteristics such as seamounts, shelf-breaks and canyons. This result support the findings of Yen et al., (2004), that demonstrated that top predators such as seabirds (e.g. Paiva et al., 2010, 2010a) and cetaceans are associated not only to bathymetric features but also to shallow water topographies. In coastal temperate regions, the combination of bathymetric features and tidal currents are commonly related to upwelling processes leading to higher productive waters capable to support greater concentrations of marine predators (e.g. Croll et al., 1998; Hunt et al., 1998; Springer et al., 1996) (Figure 10).

Oceanic environments are extremely dynamic as a result of complex interactions between physical and biological variables that change in spatial and temporal scales offering seabirds difficult conditions for gathering food (i.e. the predictability of prey location) (Weimerskirch, 2007). Thus, the location of foraging areas (S50k) in seabirds is thought to occur by following odour cues (Nevitt et al., 1995). Odour landscapes are built based on scented compounds associated with their primary prey such as pyrazines and trimethylamines (krill-related odours) and Dimethyl sulphide (DMS) (Nevitt, 2000; Nevitt and Bonadonna, 2005). DMS is a compound produced by phytoplankton when grazed by zooplankton (Dacey and Wakeham, 1986), thus associated to areas in the ocean with high productivity. In consequence, once a productive area is found (S50K), and prey capture is more predictable and profitable (Weimerskirch et al., 2007), birds engage in an area-restricted search (ARS) to identify and capture its specific prey (F50K) (Nevitt, 2000). The mechanisms birds employ for ARS are still unknown (but see (Fauchald and Tveraa, 2003), yet it may involve a combination of odour and visual cues such as following the foraging activity of conspecific (Nevitt, 2000).

## The influence of remote sensing grid and temporal resolution

Overall, 9-km grid resolutions averaging the data of one month reflected the general trends obtained on the behavior of Cory's shearwater at finer grid scales. However, in some cases such general trends were misleading. For instance, when analyzing short trips, 9-km grid resolution images suggested that the differences in chl-a concentrations in males and females was highly significant at the MCP scale and significant at S50K. Such significant differences disappeared when the analysis was done at a 0.3-km grid resolution using daily values. In long trips on the other hand, spatial scale did not influence the interpretation of differences between males and females but it showed that in areas used by females the Chl-a gradients are significantly different between MCPs and F50K.

Furthermore, the results obtained by analyzing Cory's shearwater at a 9-km grid resolution suggested that the S50K males and females use show significant differences in their SST values in short trips. This interpretation changed when the grid resolution was higher (0.3-km). Similarly, when testing for differences between males only SST values of MCPs analyzed at low resolution showed a significant difference between young and old individuals. Such difference is not significant at higher resolution grids (i.e. 0.3km). Hence, lower resolution grids could induce Type-I errors.

In summary, this study shows that during the pre-laying period males and females use areas that differ significantly in terms of Chl-a concentrations and bathymetric features. Such segregation especially occurs during long trips when females also travel significantly longer distances than males. This study also demonstrated that there is a slight trend in seabirds to not forage at the highest productive areas found within their home ranges. This trend is enhanced with the use of finer grid resolutions.



Furthermore, in some cases the use of low-resolution remote sensing images led to different interpretations of the same dataset. Therefore the use of high-resolution images is highly recommended to avoid Type I errors especially when using tracking devices that also offer high resolution data. Nonetheless, it is important to keep in mind that ocean environments represent highly dynamic systems; hence the proper understanding of its trophic dynamics still requires a lot of further research.

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**APPENDIX 1 AND 2**

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## PILOT NEST CHARACTERIZATION

To characterize nests in terms of temperature and humidity, nests were first arbitrarily grouped according to their location within the colony, orientation (in which direction was the nest entrance facing in terms of cardinal points) and exposure to the elements (wind, sun, rain, etc.). Data-loggers were then set to record 500 points every 10s and randomly (random numbers between 1-107 (nest IDs) were obtained from a calculator) placed among the nests belonging to a same group to assess for significant differences in temperature and humidity among them. The first 20 registers of each data set were removed to eliminate data recorded while manipulating the logger for starting and placing it inside the nest. Within the nest, loggers were located in places protected from direct sunlight and from the birds themselves, which could eventually sit on top of them biasing the lectures.

Similarity among nests was assessed using Spearman correlations. Only if both variables (Temperature and humidity) shared significant correlation coefficients ( $r > 0.7$ ,  $p < 0.05$ ), both were considered to be nests with common humidity and temperature characteristics and re-grouped into a common group. If one of the variables differed between nests, they were considered as nests with different characteristics, hence re-grouped separately. Once these new groups were established, temperature-humidity loggers were set to register the data used for this study: data registration set to record every five minutes and logger placed randomly in different nests every 48 hours in a way that each logger was also placed in a different group each time.



## EURING age codes

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EURING Number	Definition
0	Age unknown - only to be used if data have been lost and the ringer has no idea if a bird was a nestling or full-grown
1	Pullus (Use P not 1 for pullus on handwritten schedules as a series of 1s looks like a ditto line)
1J	Passerines only - fledged, but flying so weakly that it is obviously incapable of having flown far from the nest (include as pullus for annual totals)
2	Fully grown, year of hatching quite unknown (including current year)
2J	Fully grown, year of hatching quite unknown (including current year), still partly or completely in juvenile body plumage (rarely used)
3	Definitely hatched during current calendar year (eg first-years in autumn)
3J*	Passerines only - definitely hatched this calendar year and still partly or completely in juvenile body plumage*
4	Hatched before current calendar year - exact year unknown (eg many adults in autumn)
4I	Hatched before current calendar year - exact year unknown but definitely not full adult
5	Definitely hatched during previous calendar year (eg first-years in early spring)
5J	Definitely hatched during previous calendar year (eg first-years in early spring) still partly or completely in juvenile body plumage rarely used)
6	Hatched before last calendar year - exact year unknown (eg many adults in Spring)
6I	Hatched before last calendar year - exact year unknown but definitely not full adult
7	Definitely hatched in calendar year before last
8	Hatched three or more years ago - exact year unknown
8I	Hatched three or more years ago - exact year unknown but definitely not full adult
9	Definitely hatched three years ago
10	Hatched four or more years ago - exact year unknown
11	Definitely hatched four years ago
12	Hatched five or more years ago - exact year unknown
13	Definitely hatched five years ago
14	Hatched six or more years ago - exact year unknown
15	Definitely hatched six years ago
16	Hatched seven or more years ago - exact year unknown

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\*Because juvenile plumage - ie the feathers grown by the birds in the nest - is more easily recognised than the plumage which succeeds it, the analyst can assume a high degree of accuracy in birds aged 3J, whereas those aged 3 might possibly include a few individuals which were in fact older.