



Universidade de Aveiro  
Departamento de Biologia



Universidade de Trás-os-Montes e Alto-Douro  
Laboratório de Ecologia Aplicada



# Correlative and dynamic modelling approaches for the study of the Cory's shearwater foraging behaviour

Environmental conditions, colony attendance and  
information transfer



Beatriz Martins, 72191

**Orientador interno:** Prof. António Luís  
Universidade de Aveiro

**Orientador externo:** Prof. Mário Santos

**Co-orientador externo:** Rita Bastos  
Universidade de Trás-os-Montes e Alto-Douro

## **Agradecimentos**

Ao longo deste estágio foram várias as pessoas que de diversas formas contribuíram para a realização deste trabalho.

Em primeiro lugar, gostaria de agradecer ao Laboratório de Ecologia Aplicada, da Universidade de Trás-os-Montes e Alto Douro, pela recepção e sentimento de integração proporcionado por esta equipa, para além de todo o conhecimento partilhado ao longo deste ano.

Ao Prof. João Cabral, um agradecimento especial, por ter aceite logo desde início esta parceria e ter contribuído sempre com todo o interesse para o desenvolvimento deste estágio, cedendo o espaço e todos os recursos necessários ao seu desenvolvimento.

Aos meus orientadores, o Prof. António Luís (UA) e o Prof. Mário Santos (UTAD), pela oportunidade de aprendizagem que me concederam através deste estágio, e por todo o interesse e preocupação demonstrados. Um especial agradecimento ao Prof. Mário por toda a ajuda e disponibilidade fornecida ao longo deste trabalho, em especial durante a construção do modelo.

À Rita Bastos, por toda a orientação, disponibilidade e extrema preocupação demonstrada, desde início, no desenvolvimento deste trabalho, em associação ao seu doutoramento. Um especial agradecimento por tudo isto e por todas as oportunidades de aprendizagem que me proporcionou.

Ao projecto LIFE+ Berlengas (LIFE13-NAT\_PT\_000458) e à Sociedade Portuguesa para o Estudo das Aves (SPEA), e ao Nuno Oliveira pela cedência dos dados referentes aos *rafts*.

Ao Vitor Paiva e ao Prof. Jaime Ramos, da Universidade de Coimbra, um agradecimento especial pela cedência dos dados de *tracking* das cagaras da ilha do Corvo (Açores).

Por fim, agradeço a todas as pessoas que não foram especificadas aqui, mas que contribuíram, directa ou indirectamente, para o desenvolvimento deste estágio, e/ou para a minha estadia aqui na Bila.

## **Index**

Resumo.....	4
Abstract .....	6
1. Introduction.....	8
2. Methodology .....	11
2.1. Environmental drivers of Cory's shearwater attendance at different spatial scales .....	11
2.2. Distribution patterns and individual foraging behaviour .....	15
2.2.1. Cory's shearwater Individual-Based Model and Pattern-oriented Modelling .....	16
2.2.2 Influence of foraging mechanisms, density of foraging individuals and resources distribution in the Cory's shearwater individual foraging efficiency .....	19
3. Results .....	21
3.1. Environmental drivers of Cory's shearwater attendance at different scales – Hypothesis tests.....	21
3.1.1. Individuals attending the Berlenga island .....	21
3.1.2. Individuals attending the colony .....	22
3.1.3. Individuals attending the nests .....	22
3.2. Distribution patterns and individual foraging behaviour .....	23
3.2.1. Pattern-Oriented Modelling.....	23
3.2.2. Influence of foraging mechanisms, density of foraging individuals and resources distribution in the Cory's shearwater Individual foraging efficiency .....	26
4. Discussion.....	30
5. Conclusions.....	34
6. References.....	35

## Resumo

Os oceanos são caracterizados por fenómenos oceanográficos heterogéneos que promovem dinâmicas tróficas a escalas espaço-temporais muito variáveis. Assim, encontrar recursos alimentares é desafiante para as aves marinhas que têm de adaptar o seu comportamento de procura de alimento à variação espacial e temporal da disponibilidade de recursos no ambiente marinho. Esta adaptação é particularmente importante durante a época reprodutiva, quando as aves se comportam como *central place foragers* e necessitam de lidar com esforços adicionais associados à incubação e alimentação das crias. Neste contexto, para além das extraordinárias capacidades de navegação das aves marinhas em perceber o ambiente através de olfato, também informações de cariz pessoal e social podem possibilitar a obtenção de informação atualizada acerca da localização dos recursos alimentares, aquando da procura numa paisagem aparentemente pouco caracterizada. Assim, a procura de alimento baseada em pistas sociais, como *local enhancement*, sugere que um aumento da densidade de indivíduos aumenta a probabilidade de encontrar recursos segundo estas estratégias. Nesta perspetiva, apesar dos ciclos de regresso de indivíduos às colónias serem ainda pouco compreendidos, existem evidências que apontam para mecanismos dependentes de densidades de indivíduos como motores dos padrões cíclicos de regresso dos indivíduos às colónias de nidificação. Compreender a interação entre as estratégias individuais de procura de alimento, a distribuição dos recursos e os padrões de regresso dos indivíduos às colónias exige assim uma compreensão sólida dos mecanismos que atuam ao nível individual e que provocam padrões demográficos e espaciais observados. Neste contexto, os modelos baseados em agentes são desenhados para analisar processos *bottom-up*, onde os indivíduos respondem a estímulos internos e externos, procurando maximizar o seu *fitness* através de comportamentos adaptativos, o que leva à emergência de propriedades ao nível dos sistemas.

As cagaras são uma das espécies de aves marinhas pelágicas mais abundantes em ilhas portuguesas, que globalmente abrangem até 85% da população reprodutora mundial. Através de análises estatísticas (teste de hipóteses), técnicas de modelação baseadas em processos e Sistemas de Informação Geográfica, este trabalho pretende explorar o comportamento de procura de alimento pelas cagaras, de forma a (1) compreender o papel das condições ambientais e dos mecanismos dependentes de densidade de indivíduos que influenciam os padrões de regresso das cagaras a 3 escalas espaciais na ilha da Berlenga, e (2) analisar o papel dos diferentes mecanismos de procura de alimento como fatores determinantes para os padrões espaciais da espécie e para a eficiência individual da procura de alimento, tendo em conta a distribuição de recursos junto das colónias e a densidade de indivíduos.

De acordo com os nossos resultados, o regresso das cagaras à Berlenga, à colónia de Melreu e aos respetivos ninhos, parece ser altamente influenciado pelas condições locais ambientais, as quais parecem atuar como *proxies* da disponibilidade de recursos e do sucesso de procura individual, explicando parcialmente o regresso dos indivíduos aos locais de nidificação. Adicionalmente, mecanismos dependentes de densidades parecem ocorrer com maior expressão a escalas locais (colónia e ninhos), podendo a sincronização dos indivíduos ser explicada por contactos sociais relevantes e/ou mecanismos de cooperação entre indivíduos da mesmo sub-colónia. Além disso, a correlação residual existente entre o regresso dos indivíduos à ilha e o regresso dos

indivíduos à colónia ou aos ninhos pode sustentar mecanismos de comportamento desconhecidos que acuem entre os indivíduos de diferentes sub-colónias estabelecidas na mesma ilha.

A abordagem correspondente ao *Pattern-oriented modelling* permitiu avaliar qual mecanismo de procura alimentar (*Correlated random walk*, procura olfativa ou procura olfativa com visão) melhor reproduziu um conjunto de padrões observados em indivíduos reais monitorizados. De um modo geral, o *correlated random walk* conseguiu retratar de uma forma mais realista a distribuição espacial das cagarras na área circundante da ilha do Corvo. No entanto, a procura olfativa com visão verificou-se mais precisa na reprodução dos padrões espaciais do uso dos habitats ao nível individual. No que diz respeito ao sucesso individual, um aumento significativo do *fitness*, à medida que os mecanismos de procura de alimento se tornam mais complexos, parece indicar que estratégias olfativas e/ou sociais promovem eficácia no encontro de alimento, especialmente quando os recursos são escassos junto às colónias. Os nossos resultados sugerem ainda que os mecanismos que sustentam o *local enhancement* são mais eficazes em casos de maiores densidades populacionais, nomeadamente através do aumento da probabilidade de encontro com indivíduos que se estão a alimentar. Além disso, as aves que procuram alimento em condições mais desfavoráveis parecem ser mais dependentes dos conspecíficos para encontrar áreas de alimentação, comparativamente a aves que nidificam em áreas mais favoráveis.

Como perspetivas de investigação futura aponta-se a inclusão de mecanismos de procura de alimento adicionais, nomeadamente aprendizagem social através de rafts e aprendizagem pessoal através da memória. Adicionalmente, será também importante explorar cenários referentes a ambientes dinâmicos, de maneira a investigar o papel da variabilidade ambiental nos padrões de distribuição espacial das cagarras. Ainda nesta perspetiva, uma abordagem baseada na Teoria de Forrageamento Ótimo, assente em balanços entre gastos e ganhos energéticos, pode também revelar conhecimento adicional acerca do comportamento adaptativo das cagarras face à variabilidade espaço-temporal da disponibilidade de recursos, sucesso reprodutor e mecanismos envolvidos nos padrões de regresso dos indivíduos às colónias.

**Palavras-chave:** cagarras; *Calonectris borealis*; condições ambientais; modelos baseados em agentes; procura de alimento; regresso à colónia; sucesso alimentar; teste de hipóteses; transferência social de informação.

## **Abstract**

Oceans are characterized by heterogeneous oceanographic phenomena that promote trophic dynamics at variable spatial-temporal scales, thus finding food resources in the marine environment is challenging for seabirds which must adapt foraging behaviour to cope with spatial and temporal variation in resource availability. This is particularly important during reproduction when birds are central place foragers and have to cope with additional efforts associated with incubation and chick provisioning. In this context, apart from the seabirds' extraordinary navigation capacities to percept the environment through olfactory senses, also personal and social information may allow individuals to obtain updated foraging information about food resources location in featureless seascapes. Therefore, network (social) foraging, such as local enhancement, suggest that the increasing density of foraging birds improves the probability of discovering food patches under these strategies. In this perspective, although attendance cycles in seabird colonies are still poorly understood, evidences point to density-dependent mechanisms driving cyclic patterns of individuals' attendance at their nesting colonies. Understand the interaction between foraging strategies, resource distribution and patterns of colony attendance therefore require a solid understanding of the individual-level mechanisms that give rise to observed demographic and spatial patterns. In this context, Individual-Based Models (IBMs) are designed to undertake bottom-up simulations, in which individuals respond to internal and external environments by seeking to maximize 'fitness' through adaptive behaviour, leading to the emergence of system level properties.

The Cory's Shearwater is one of the most abundant pelagic seabird species breeding in Portuguese islands, which globally comprise up to 85% of the world breeding population. Using statistical (Hypotheses test), process-based modelling techniques (IBMs) and Geographic Information Systems, this work intends to explore the Cory's shearwater foraging behaviour in order to (1) understand the role of environmental conditions and density-dependent mechanisms influencing the Cory's shearwater attendance patterns at three spatial scales in the Berlenga Island and (2) to address the role of different foraging mechanisms as drivers of the species' spatial patterns and individual foraging efficiency, taking into account the distribution of resources around breeding colonies and the density of foraging individuals.

According to our results, the returning of Cory's shearwaters at the Berlenga Island, the Melreu colony and respective nests appeared to be highly influenced by environmental conditions, which may be acting as proxies of resources availability and individual foraging success, thus partially explaining the returning of individuals to nesting sites. Additionally, density-dependent mechanisms seem to occur with higher expression at local scales (nests and colony), in which the synchronization of individuals may be influenced by relevant social contacts and/or cooperation mechanisms among individuals from the same sub-colony. Furthermore, the residual correlation between birds attending the island and birds attending the colony or nests may underpin unknown behavioural mechanisms acting among individuals from different sub-colonies established in the same Island.

The Pattern Oriented Modelling approach allowed to evaluate which foraging decision rules (Correlated Random Walk, olfactory-search or olfactory-search with vision) caused the IBM model to best reproduce a range of patterns observed in real tracked individuals. In general, the correlated

random walk was able to capture in a realistic way the overall spatial distribution of Cory's shearwaters foraging in the surrounding of the Corvo Island. However, the olfactory search with vision was more precise in reproducing spatial patterns of habitat use at the individual level. Regarding individual foraging success, a significant increase in fitness as foraging mechanisms become more complex seems to indicate that olfactory and/or network foraging strategies promote efficiency in discovering food patches, especially when resources are scarce around breeding colonies. Our results still suggest that the mechanisms underpinning local enhancement are more effective under increasing population densities, namely by improving the probability of encounters with successful feeders. Furthermore, birds foraging in poorer conditions seem to be more dependent on conspecifics to find food patches than birds breeding in more profitable areas.

Future research perspectives should be directed to the inclusion of additional foraging mechanisms, namely social learning through rafts and personal learning through memory. Additionally, it would be interesting to explore dynamic environmental scenarios in order to investigate the role of spatio-temporal variability in the Cory's shearwaters spatial distribution patterns. An approach following the unified foraging theory, based on trade-offs between energetic expenses and benefits of movements, could also give important insights about the adaptive behaviour of Cory's shearwaters to spatio-temporal variability in resources availability, breeding success and the mechanisms underpinning the patterns of colony attendance.

**Keywords:** *Calonectris borealis*; colony attendance; Cory's shearwater; environmental conditions; feeding success; foraging behaviour; hypothesis test; individual-based models; social information transfer.

## 1. Introduction

Oceans are extremely heterogeneous and dynamic environments, determined by oceanographic phenomena such as ocean currents and upwelling events that promote trophic interactions at variable spatial-temporal scales (Grémillet & Boulinier, 2009; Weimerskirch, 2007). Finding food resources in the ocean is therefore challenging for top-predators such as seabirds, since the uncertainty in the distribution and abundance of prey in the marine environment (Grémillet & Boulinier, 2009; Weimerskirch, 2007) makes food resources patchy and difficult to predict and locate (Weimerskirch, 2007). In this context, at the global scale, the marine systems can be categorized into two broad distinct zones, characterized by different levels of productivity and predictability of resources location, the neritic and the oceanic zone (Lalli & Parsons, 1997). This classification is based on depth and distance from landmasses: neritic systems refers to inshore water shallower than 200 meters in depth (low bathymetry, continental shelf), whereas oceanic systems refers to offshore waters in areas deeper than 200 meters (high bathymetry, oceanic shelf) (Lalli & Parsons, 1997). These two marine systems are also associated with different ecological characteristics associated with dissimilar oceanographic phenomena. Neritic systems are usually related with major upwelling events that drive more constant conditions associated with shallow waters and enhanced primary production. In this way, neritic systems present more profitable foraging grounds for marine top predators (Paiva et al., 2010). On the other hand, oceanic systems are usually characterized by lower marine productivity and higher environmental stochasticity, providing less predictable foraging areas for top predators (Paiva et al., 2010). Therefore, seabirds must adapt foraging behaviours to cope with spatial and temporal variations in resource availability (Paiva et al., 2010; Weimerskirch, 2007). This adaptation is especially important during reproduction when birds are central place foragers and have to cope with additional efforts associate to incubation and chick provisioning (Burke & Montevecchi, 2009).

The Cory's Shearwater (*Calonectris borealis*, Cory 1881) is one of the most abundant pelagic seabird species breeding in the Portuguese archipelagos of Azores, Madeira and Berlengas, which comprise up to 85% of the world breeding population (BirdLife International, 2017). Population-based studies of Cory's shearwaters indicate divergences in foraging strategies of individuals breeding under different environmental conditions (i.e. oceanic versus neritic environments) (Paiva et al., 2010a). Cory's shearwaters breeding under oceanic environments (e.g. Azores archipelago) present a dual-foraging strategy in which individuals alternate between short foraging trips (up to 4 foraging days), mainly used to find food for the chicks and long foraging trips to suppress their own nutritional requirements (up to 20 foraging days) (Magalhães et al., 2008). On the other hand, individuals breeding under neritic conditions (e.g. Berlengas archipelago) tend to perform a unimodal foraging strategy, characterized by almost exclusive short foraging trips that allow simultaneously to invest in reproduction while ensuring their own survival (Magalhães et al. 2008; Paiva et al., 2010a; Paiva et al., 2010). Therefore, Cory's shearwaters are able to adjust foraging

strategies to cope with the environmental conditions surrounding their breeding colonies (Magalhães et al., 2008; Paiva et al., 2010a; Weimerskirch et al., 1994).

While foraging at sea, several foraging mechanisms allow seabirds to update information concerning food resources location, thus contributing to an increase in efficiency, foraging success and, consequently in the reproductive success (Thiebault et al., 2014). Apart from the seabirds' extraordinary navigation capabilities to percept the environment through senses, such as olfactory cues (Nevitt et al., 2008), individual memory and shared information among individuals may also allow increased accuracy in food resources location within featureless seascapes (Thiebault et al., 2014). This information can be obtained through personal interaction with the environmental (short-term recall and memory) or through interaction with conspecifics (social information) (Danchin, 2004). In terms of network foraging (social mechanisms), breeding colonies may work as information centres, where individuals may have the opportunity to obtain (and share) information, namely by monitoring the behaviour of successful foragers returning and/or leaving the colony (Boyd et al., 2016; Thiebault et al., 2014; Weimerskirch et al., 2010). One hypothesis is that this process occurs mainly in rafts, which are aggregations of individuals at sea, near the colony (Weimerskirch et al., 2010). In some seabird species, such as Guanay cormorants, rafts appear to work as a compass that consecutively aligns according to the bearings of the successful individuals (Weimerskirch et al., 2010). When foragers find a food patch, they return to the colony according to a straight linear route, representing a reliable foraging bearing (Weimerskirch et al., 2010). If individuals return from a different direction (from a new feeding patch, for example), compass raft adjusts its direction according to the new returning bearing (Weimerskirch et al., 2010). Furthermore, social information can also be obtained through local enhancement, which is a mechanism involving the attraction of foragers to locations where other individuals are feeding, thus working as an indicator of potential food resources (Boyd et al., 2016; Weimerskirch, 2007). This kind of information works through visual foraging cues, also associated with monitoring of conspecifics' behaviour (Boyd et al., 2016). The local enhancement hypothesis (Buckley, 1997; Mock et al., 1988) suggests that the increase in density of foraging birds and other predator aggregations improves the probability of discovering unpredictably distributed food patches (Thiebault et al., 2014; Boyd et al., 2016). Still in this context, throughout the nesting season, seabirds show cyclic patterns of individuals' attendance at their nesting colonies. In Cory's shearwaters, the number of individuals visiting the colony along the breeding season varies according to cyclic or acyclic patterns (Granadeiro et al., 2009). The reason for these attendance cycles is still poorly understood nevertheless, according to Granadeiro et al. (2009), larger colonies tend to present well-defined cyclic attendance patterns (e.g. Azores and Selvagem Grande) contrarily to smaller colonies (e.g. Berlenga and Selvagem pequena). These findings support the idea that attendance cycles facilitate encounters between socially relevant contacts, thus being more likely to occur in large and dense colonies (Granadeiro et al., 2009).

Understand and predict how breeding individuals adapt foraging behaviour to cope with spatial and temporal variation in resource availability is therefore a key question in ecology and conservation (Magalhães et al., 2008; Paiva et al., 2010; Weimerskirch, 2007). In this context, the

comprehension of the interaction between behavioural strategies and resource distribution requires a solid knowledge about the individual-level mechanisms that give rise to observed demographic and spatial patterns. For this, we should integrate information on the specie's adaptive behaviours and habitat selection, movement ecology, and the responses to dynamic environments. In this context, Individual-Based Models (IBMs) are designed to undertake simulations based on bottom-up structure and functioning: individuals respond to internal and external environments by seeking to maximize 'fitness' through adaptive behaviour, leading to the emergence of system level properties (Grimm & Railsback, 2005). This allows the processes and mechanism behind the observed patterns to be revealed, including the comprehension of how animals perceive, learn and adapt to their environment (DeAngelis & Mooij, 2005).

Using statistical, process-based modelling techniques and Geographic Information Systems, this work intends to explore the Cory's shearwater foraging behaviour and spatial distribution, aiming to:

- **Understand how environmental conditions and density-dependent mechanisms may influence the individuals' attendance at three spatial scales.**
  - (1) How do environmental conditions influence the returning of individuals to the island, colony and nests?
  - (2) To what extent density-dependent mechanisms are related with the returning of individuals to the island, the colony and the nests?
  
- **Address the role of different foraging mechanisms as drivers of species' spatial patterns and individual foraging efficiency, taking into account the distribution of resources around breeding colonies and the density of foraging individuals.**
  - (3) To what extent the use of different foraging mechanisms may affect the Cory's shearwater distribution patterns and habitat use?
  - (4) How does the use of olfactory search and social information (local enhancement) may affect the feeding efficiency of individuals foraging in different environmental conditions?
  - (5) What is the interplay between the density of foraging individuals and the effectiveness of local enhancement in different scenarios of resources distribution around breeding colonies?

## 2. Methodology

### 2.1. Environmental drivers of Cory's shearwater attendance at different spatial scales

The Berlengas archipelago is located near the Portuguese coastline (western continental shelf of the Iberian Peninsula), at 8.7 km from Cape Carvoeiro in the municipality of Peniche (Figure 1). The archipelago comprises the Berlenga Island (Figure 2), the largest island (78.8 ha), and two groups of smaller rocky islets, "Farilhões" and "Estelas". The area adjacent to this archipelago is characterized by a highly productive neritic environment of shallow waters with low temperatures and high primary productivity (Paiva et al., 2010). From a total of 980-1070 breeding pairs nesting in the Berlengas archipelago, 310 pairs are estimated to breed in the Berlenga Island itself (Lecoq et al., 2011).

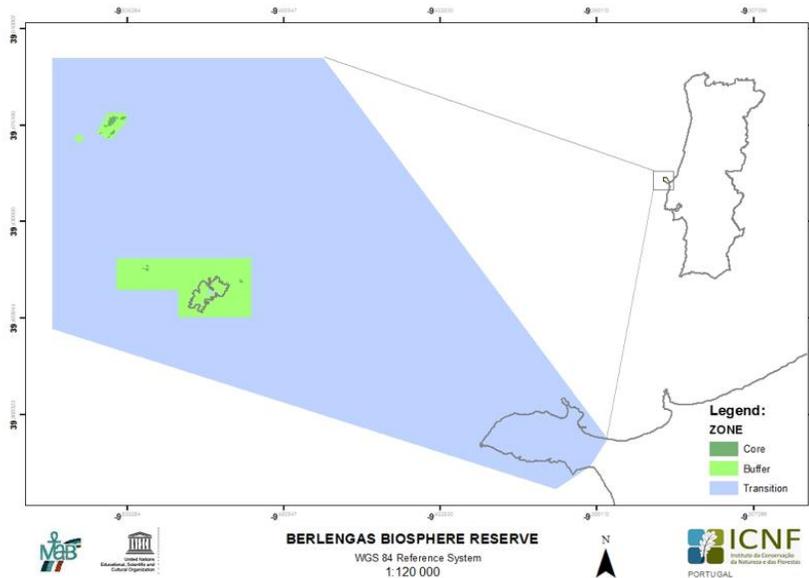


Figure 1 The Berlengas archipelago located in the Portuguese coast. Map obtained from: <http://www.icnf.pt/portal/naturaclias/ei/resource/img/mab/rb-berleng-map/view> (ICNF, n.d.).

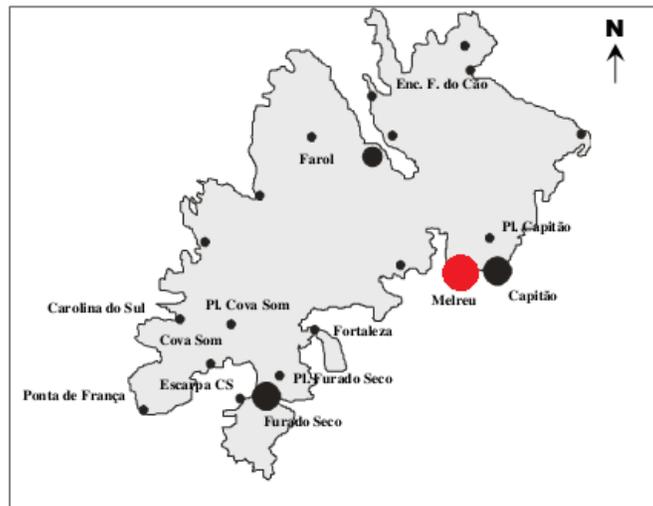


Figure 2 The Berlenga Island with the Melreu's colony highlighted in red. Map obtained from: Lecoq (2010).

Bird counts were performed at the Berlenga Island, from September to November 2015 and from May to October 2016 (on average during a week per monitored month) at three spatial scales, namely the Berlenga Island, the Melreu colony and the nests from the Melreu colony. To assess an estimate of the total abundance of birds attending the Island, individuals were counted daily at dusk in various points distributed in the Berlenga Island. This data included individuals from different colonies that congregated on rafts at the end of the day, reflecting a global count of individuals attending the Berlenga Island. At the colony level, all individuals seen out of the nests and spotted inside the nests were counted, along a transect performed every night throughout the Melreu colony.

In order to understand the influence of environmental conditions in the presence/abundance of birds at the three selected scales, different environmental data were collected (Table 1). Daily environmental data on wind speed, wave height, wave period, temperature, precipitation and cloud cover were obtained for Peniche in the same weeks when bird counts were performed (<https://www.windguru.cz/>). Furthermore, the upwelling index, which measures the volume of water that upwells along the coast (i.e. the amount of offshore transport of surface waters due to wind fields), was collected for the Cape Roca (<http://www.indicedeafloramiento.ieo.es/afloramiento.en.html>). Lunar information, namely moonrise, moonset and fraction of moon illuminated, was also extracted (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services>).

Table 1 The environmental variables used to infer the Cory's shearwater attendance patterns, including units of measure, frequency and time span of extraction (Time series), specific measurements and main data sources.

Environmental variables	Units	Time series	Measurement	Database
Wind speed	m/s	Daily, 3 hours span (hours selected: 10-22h).	Wind speed 10 meters above surface.	<a href="https://www.windguru.cz/">https://www.windguru.cz/</a>
Wave height	m		Wave average height of one-third of the highest waves.	
Wave period	s		Period between wave crests in seconds.	
Temperature	° C		Temperature 2 meters above ground.	
Precipitation	mm/3h		Precipitation millimetres accumulated for 3 hours.	
Cloud cover	%		Global level of cloud cover (low, middle and high clouds all together).	

<b>Upwelling index</b>	$m^3 \cdot s^{-1} / km$	Daily, 6 hours (hours selected: 12-18h).	Volume of upwelled flow estimated per kilometre of coastline, depending on latitude and wind stress and direction.	<a href="http://www.w.indicedeafloremiento.ieo.es/a">http://www.w.indicedeafloremiento.ieo.es/a</a>
<b>Moonrise</b>	Hour	Daily.	Time of day when the moon is on the horizon. No account is taken of the moon's phase, or in other words, the moon is always observed as a disk in the sky.	<a href="http://www.usno.navy.mil/USNO/astronomical-applications/data-services">http://www.usno.navy.mil/USNO/astronomical-applications/data-services</a>
<b>Moonset</b>	Hour	Daily.		
<b>Fraction of moon illuminated</b>	%	Daily, 12 hours.	Percentage of moon surface illuminated (i.e. 100 % full moon and 0 % new moon).	

The dependent variables correspond to the Cory's shearwater abundance, expressed in bird numbers. The independent variables are expressed by the environmental parameters that characterize the Berlenga surrounding in terms of oceanographic conditions. Furthermore, in order to analyse the inter-dependence between birds attending the Island, the colony and the nests, these variables were also tested as predictors of each other. In order to avoid multicollinearity, the selected predictors for the Cory's shearwater abundance were tested for pairwise correlation, using Spearman's rho correlation coefficient, and only predictors with correlation lower than 0.7 (Elith et al., 2006; Wisz & Guisan, 2009), and Generalized Variance Inflation Factor lower than 5 were considered (Neter et al., 1996).

For each of the response variables, we ran a hypothesis test considering different competing models of explanatory variables, compared with a null model randomly settled (Vicente et al., 2010) (Tables 2, 3 and 4). Cory's shearwater abundances follow an over-dispersion Poisson distribution (variance/mean  $\gg 1$ ) (Lynch et al., 2014; McMahon et al., 2016), which is relatively common for count data in ecology (Ver Hoef & Boveng, 2007) and particularly in census of colonial seabird with high detection probability (Lynch et al., 2014). Considering this, we assumed a quasi-Poisson distribution to ensure a better fit of the overall variance-mean relationship (e.g. Ver Hoef & Boveng, 2007). Rather than a single best model, we fit a set of competing Generalized Linear Models (GLMs) within a multi-model inference framework (MMI; Burnham & Anderson, 2002) to assess how well each model was supported by the data. We used the corrected Akaike Information Criterion (AIC; Akaike, 1973) for small sample sizes (AIC<sub>C</sub>; Shono, 2000), as recommended when the ratio between  $n$  (the number of observations used to fit the model) and  $K$  (the number of parameters in the largest model) is  $< 40$  (Burnham & Anderson, 2002; Shono, 2000). For comparisons among models we calculated the AIC<sub>C</sub> difference, where  $D_i = AIC_{C \text{ initial}} - AIC_{C \text{ minimum}}$  (where: AIC<sub>C</sub> initial is second-order AIC for each competing model, and AIC<sub>C</sub> minimum is the estimate of relative, expected

Kullback–Leibler distance information for the best model in the set, given the data; Burnham & Anderson, 2002). Using the  $D_i$  we derived the Akaike weights ( $w_i$ ), interpreted as the probability that a candidate model will be the best approximating and most parsimonious model given the data and the set of models. These weights are scaled between zero and one, and represent the evidence for a particular model as a proportion of the total evidence supporting all models (Burnham & Anderson, 2002). Finally, we calculated the Nagelkerke's  $R^2$  (Guisan & Zimmermann, 2000) to estimate the models' explanatory power. All statistical analysis were performed using the software R 3.3.2 (R Core Team, 2017).

Table 2 Hypothesis test to infer the returning of Cory's shearwaters to the Berlenga island. Specific hypotheses and related competing models with the predictors used in each model.

<b>Response variable: individuals attending the Berlenga island.</b>	
<b>Hypothesis</b>	<b>Competing models and explanatory variables</b>
<b>H<sub>1</sub></b>	Environmental variables: wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index.
<b>H<sub>2</sub></b>	Individuals attending the colony.
<b>H<sub>3</sub></b>	Individuals attending the nests.
<b>H<sub>4</sub></b>	Environmental variables and individuals attending the colony.
<b>H<sub>5</sub></b>	Environmental variables and individuals attending the nests.
<b>H<sub>6</sub></b>	Null model (randomly settled).

Table 3 Hypothesis test to infer the returnin of Cory's shearwaters to the Melreu colony. Specific hypotheses and related competing models with the predictors used in each model.

<b>Response variable: individuals attending the Melreu colony.</b>	
<b>Hypothesis</b>	<b>Competing models and explanatory variables</b>
<b>H<sub>1</sub></b>	Environmental variables: wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index.
<b>H<sub>2</sub></b>	Individuals attending the Berlenga island.
<b>H<sub>3</sub></b>	Individuals attending the nests.
<b>H<sub>4</sub></b>	Individuals attending the Berlenga island and nests.
<b>H<sub>5</sub></b>	Environmental variables and individuals attending the Berlenga island.
<b>H<sub>6</sub></b>	Environmental variables and individuals attending the nests.
<b>H<sub>7</sub></b>	Environmental variables and individuals attending both Berlenga island and the nests.
<b>H<sub>8</sub></b>	Null model (randomly settled).

Table 4 Hypothesis test to infer the returning of Cory's shearwaters to the Melreu nests. Specific hypotheses and related competing models with the predictors used in each model.

Response variable: individuals attending the Melreu nests.	
Hypothesis	Competing models and explanatory variables
H <sub>1</sub>	Environmental variables: wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index.
H <sub>2</sub>	Individuals attending the Berlenga island.
H <sub>3</sub>	Individuals attending the colony.
H <sub>4</sub>	Individuals attending the Berlenga island and the colony.
H <sub>5</sub>	Environmental variables and individuals attending the Berlenga island.
H <sub>6</sub>	Environmental variables and individuals attending the colony.
H <sub>7</sub>	Environmental variables and individuals attending both the Berlenga island and the colony.
H <sub>8</sub>	Null model (randomly settled).

## 2.2. Distribution patterns and individual foraging behaviour

In order to analyse role of behaviour-based mechanisms as drivers of the Cory's shearwater' spatial patterns and individual foraging efficiency, an Individual Based Model was developed to simulate the species foraging behaviour, taking into account different foraging mechanisms associated with an increasing in the individuals' navigation capacities (i.e. olfaction and vision). The hypotheses postulated were analysed through a Pattern-Oriented Modelling (POM) approach that allowed to analyse/validate the behavioural mechanisms that best describe the spatial distribution of real Cory's shearwaters. In fact, POM uses a set of observed patterns of real data as foundation for compare, teste and validate the model, thus the closest the simulated patterns are to the real data, the accurate a IBM model is considered (Railsback & Johnson, 2011). Therefore, we used as baseline the study from Ceia et al. (2015) to design and analyse our model performance. In this context, the Cory's shearwater IBM was developed to address the mechanisms underpinning foraging behaviour of real individuals from 2 neighbouring sub-colonies of Cory's shearwater breeding in the Corvo Island (Azores) (Figure 3 and 4), during short foraging trips ( $\leq 1$  day trip duration, 216 km from colony) in August 2010, where 43 breeding individuals were tracked using GPS devices with recorded positions every 5 minutes (Ceia et al., 2015)

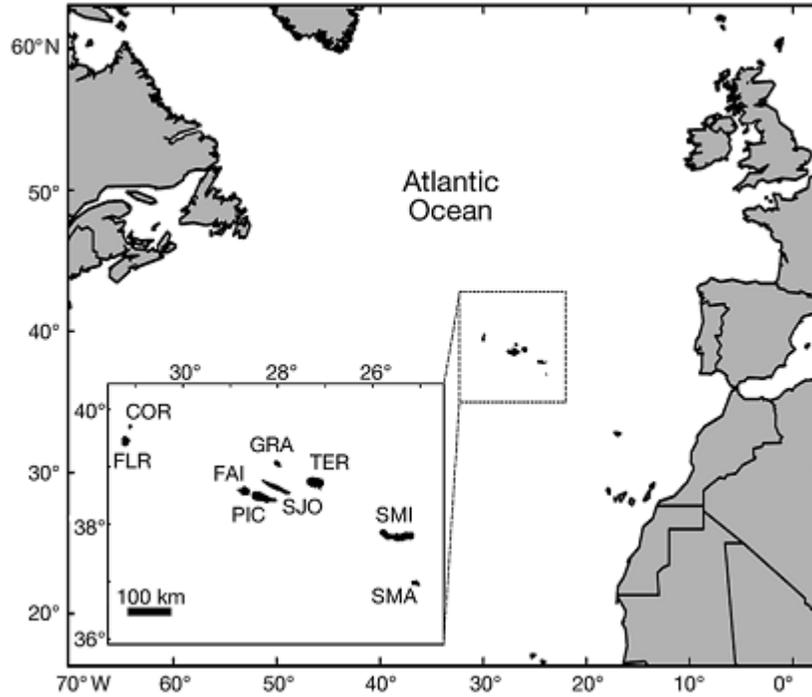


Figure 3 Localization of the Azores Archipelago and the Corvo Island (COR). Other islands: FLR = Flores; GRA = Graciosa, FAI = Faial, PIC = Pico, SJO = São Jorge, TER = Terceira; SMI = São Miguel, SMA = Santa Maria. Map obtained from: Magalhães et al. (2008)

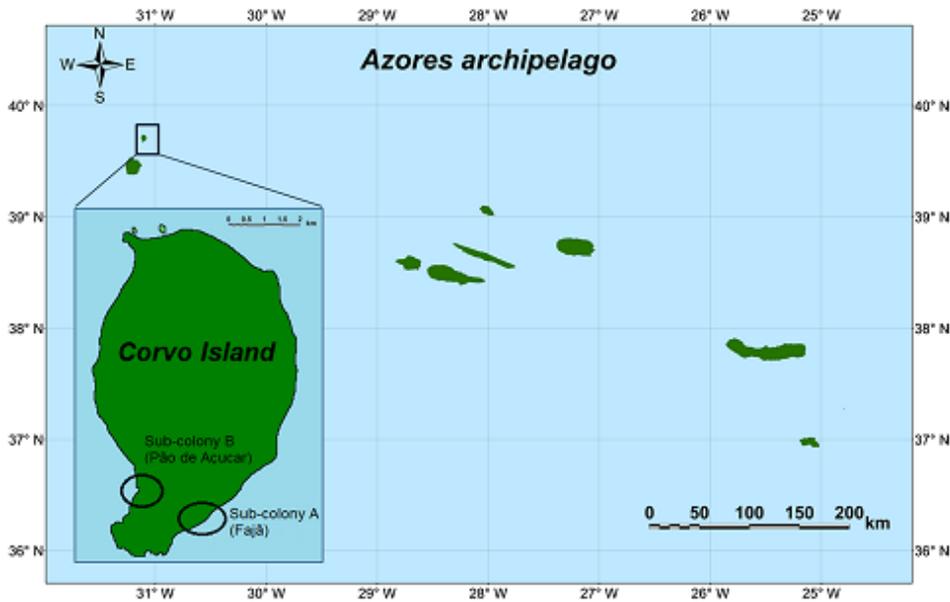


Figure 4 Localization of the Corvo Island in the Azores archipelago, including the localization of the 2 sub-colonies of Cory's shearwater: sub-colony A (Fajã) located at the eastern side of the island, and sub-colony B (Pão de Açúcar) at the western side. Map obtained from: Ceia et al., 2015.

### **2.2.1. Cory's shearwater Individual-Based Model and Pattern-oriented Modelling**

*Netlogo* (Wilensky, 1999) is a suitable software for IBMs development, based on a programming language derived from Logo (Berryman & Angus, 2010). It includes different components, essentially agents (individuals) and patches (environment) (Berryman & Angus, 2010), which can have their own programmable characteristics. Furthermore, Netlogo also includes an interface that allows the developer to control parameters and create graphs to monitor the studied metrics (Berryman & Angus, 2010).

The Cory's shearwater IBM was developed in order to analyse the spatio-temporal distribution of virtual Cory's shearwaters throughout a day of foraging at sea, considering 2 separated colonies settled in the same island (Figure 4). Two types of conceptual entities were modelled: patches (unit cells) that compose the modelled seascape, and mobile entities corresponding to Cory's shearwater individuals. The simulated environment totalizes an area of 147 456 km<sup>2</sup> (384 km × 384 km), composed on a grid of unit cells with 16 km<sup>2</sup> (4 km × 4 km) that corresponds to the surrounding of the Corvo island (39°40'N 31°06'W, Azores). The time unit used was 5 minutes and each simulation lasts 10 hours (120 time units), assuming the period corresponding to 1 foraging day.

The foraging mechanisms included in the Cory's shearwater IBM were:

H0: virtual birds that forage according to a correlated-random searching strategy;

H1: virtual birds that forage according to an olfactory-based searching strategy (hereafter, olfactory search);

H2: virtual birds that forage according to an olfactory-based searching strategy and interact with each other through local enhancement (visual contact with successful feeders).

These three hypotheses underlie two ways of modelling animal movements (the movement decisions that cause an agent to act on, and react to, the environment around it): (H1) an approach based on the geometric real characteristics of the animal movements (step length and turning angle), such as a Correlated Random Walk (CRW); (H1 and H2) an approach based on the real geometric characteristics of the animal movements (step length and turning angle) combined with a habitat selection approach based on perceptual landscape characteristics (Biased Correlated Random Walk; BCRW).

In relation to the CRW, geometric characteristics of real Cory's shearwater movements were extracted from 1-day foraging trips around Corvo, during August of 2010. These data allowed to assign specific flight characteristics, particularly turning angles and speed flights for different movement behaviours, such as Area Restricted Search and travelling. In fact, when exploring resources at sea, seabirds should cope with the hierarchical spatial distribution of resources, searching for prey that are clustered from fine to large scale in nested unities (Fauchald, 1999). For this reason, individuals adopt a typical movement composed of numerous short legs, known as Area Restricted Search (ARS), interspersed with series of directed longer legs (Weimerskirch, 2007). ARS

appear as an individual reaction to changes in the resources availability and distribution, by increasing the residence time in the productive patch rather than where resources are scarce (Fauchald & Tveraa, 2003). Consequently, during ARS, birds reduce speed and increase turning rate, as a response to increased productivity in a restricted area (Weimerskirch, 2007).

In what concern to the Biased Correlated Random Walk (thereafter mentioned as olfactory search), we assumed that virtual birds can sense on a maximum range of 20 kilometres ahead (based on wandering albatross evidences, i.e. Nevitt et al., 2008), assuming any wind direction on a 180° perception angle. Additionally, individuals can have the capacity of interact with each other through local enhancement (visual contact with successful feeders). This option can be linked with any foraging mechanism described above and virtual individuals were assumed to have visual acuity up to 10 kilometres ahead (based on Cape gannets evidences, i.e. Thiebault et al., 2014) on a vision radius of 148 ° (based on Manx shearwater evidences, i.e. Martin & Brooke, 1991). The conceptual diagram of the Cory's shearwater IBM is presented in Figure 5.

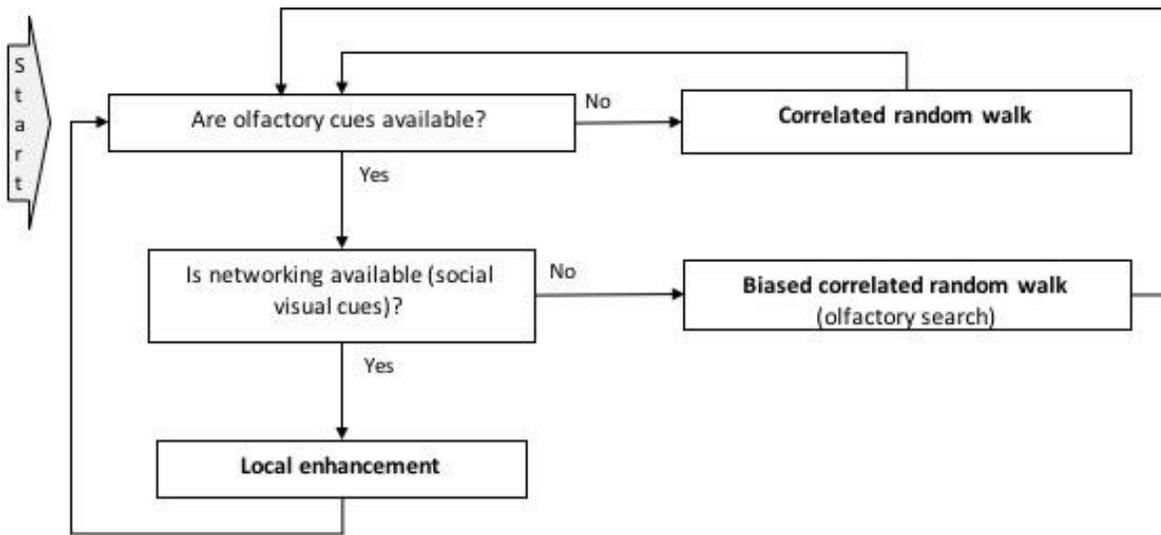


Figure 5 Conceptual diagram of the Cory's shearwater IBM. Local enhancement is prioritized over olfactory search. If visual cues are not available, individuals engage in olfactory search. In case of neither visual or olfactory cues are available, virtual birds follow a correlated random walk.

To characterize the habitat suitability for virtual Cory's shearwaters foraging in the vicinities of the Corvo Island, the thresholds described by Ceia et al (2015) on concentration of chlorophyll-a ( $\text{mg m}^{-3}$ ), sea surface temperature ( $^{\circ}\text{C}$ ) and bathymetry (m) were used to identify suitable feeding patches for the species. Therefore, the environmental scenario considers monthly average values of concentration of chlorophyll-a and sea surface temperature during August 2010 (in accordance with Ceia et al., 2015). Bathymetry data was extracted from a grid of  $0.01^{\circ}$  (approx. 1 km) from <http://www.ngdc.noaa.gov/mgg/global/global.html>, whereas Chl *a* and SST data were downloaded for a spatial resolution of  $0.04^{\circ}$  (approx. 4 km) of Aqua-MODIS mapped products from <http://oceancolor.gsfc.nasa.gov/cgi/13>. The obtained layers were imported into NetLogo and were

used to characterize patches. Therefore, for each time unit spent on a feeding patch, virtual individuals were programmed to gain 1 energy unit. In this way, energy is assumed as a proxy of time spent on profitable areas.

To evaluate which foraging mechanism best characterise the Cory's shearwaters spatial patterns of habitat use, we analysed whether each rule caused the model to reproduce a range of patterns observed in real tracked individuals from Corvo in 2010 (Ceia et al., 2015). The simulated data were exported from NetLogo into Geographic Information System (GISs) as shapefiles. The contrasted patterns include changes in:

- maximum and mean distance from colony (1-day foraging trip);
- mean bearing from the colony to the most distant foraging locations;
- mean geographic position (i.e. latitude and longitude) of foraging areas;
- 25, 50 and 75 % density contour areas, and respective areas (km<sup>2</sup>), calculated by fixed kernel density (75, 50 and 25 % FKD) (*adehabitat* package;  $h = 0.039$ , grid = 500; Calenge, 2006) in R 2.14.0 (R Core Team, 2017).

In order to ensure comparisons between simulated and real tracking data (20 real individuals from sub-colony A + 20 real individuals from sub-colony B; Ceia et al., 2015), 20 virtual individuals from each modelled sub-colony were selected. Since local enhancement is driven by conspecific aggregations, thus being influenced by increasing densities of foraging individuals (Thiebault et al., 2014), 1000 virtual individuals were assumed as a valid sub-colony size (Oppel et al., 2014). Finally, multiple non-parametric comparison tests (Kruskall-Wallis test and Dunn test) were used to detect significant differences in the resultant patterns from the different foraging mechanisms considered.

### **2.2.2 Influence of foraging mechanisms, density of foraging individuals and resources distribution in the Cory's shearwater individual foraging efficiency**

In order to assess the influence of the different foraging mechanisms in the Cory's shearwater individual foraging efficiency (average intake per individual), taking into account the resource distribution around the colony, 3 hypothetic environmental scenarios were designed:

1. Abundant resources distributed around the breeding colony
2. Intermediate resources distributed around the breeding colony
3. Scarce resources distributed around the breeding colony

In this context, for each scenario and foraging mechanisms considered (correlated random walk / olfactory search (BCRW) / olfactory search (BCRW) with vision), 100 simulations were run, taking into account an incremental number of virtual individuals for the simulated colony (100, 500 and 2000 individuals). All these simulations were performed on *BehaviorSpace* and the metric used was average energy intake per individual in a foraging day per sub-colony. *BehaviorSpace* is a software tool integrated with *Netlogo* that allows users to perform many experiments at once, while varying the model's settings and parameters, and specifying which values, ranges and thresholds to

simulate. The generated data were then submitted to multiple comparison tests (Kruskall-Wallis test and Dunn test) to detect significant differences in the foraging efficiency of virtual individuals, taking into account the different foraging mechanisms and total number of individuals considered in the 3 environmental scenarios selected.

### 3. RESULTS

#### 3.1. Environmental drivers of Cory's shearwater attendance at different scales – Hypothesis tests

The final set of explanatory environmental variables used in the hypothesis test for the Cory's shearwater attendance at different scales were wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index. The partial regression coefficients are displayed in brackets.

##### 3.1.1. Individuals attending the Berlenga island

The hypothesis test showed that the number of individuals attending the Berlenga Island was best explained (~35% explanatory power) by the environmental variables and the individuals attending the colony (best model – H<sub>4</sub>) (Table 5). Since the number of individuals attending the colony was highly correlated with the number of individuals attending the nests (Spearman test > 0.7), these variables were used as exclusively explanatory predictors for this response variable (thus only 6 hypotheses were tested for individuals attending the Berlenga Island). In this context, individuals attending the colony (H<sub>2</sub>) or individuals attending the nests (H<sub>3</sub>) appeared to have little influence on the response variable (4.6% and 4.3%, respectively), indicating that individuals attending the Berlenga Island were mainly influenced by environmental variables (H<sub>1</sub> – 27.7%). Considering the model selected (H<sub>4</sub>), the response variable was positively influenced by individuals attending the colony (0.009), temperature (0.202), precipitation (0.574) and cloud cover (0.016) and negatively influenced by wind speed (-0.028), wave height (-0.270), wave period (-0.041) and upwelling index (-0.0002).

Table 5 Results of information-theoretic-based model selection for Cory's shearwaters returning to the Berlenga Island: the number of model parameters (K), Nagelkerke's R<sup>2</sup> (R<sup>2</sup>), AIC<sub>c</sub> difference (Di) and Akaike weights (wi). In bold, the best competing model to explain the response variable.

Individuals attending the Berlenga island				
Hypothesis	K	R <sup>2</sup>	Di	wi
H <sub>1</sub> . Environmental variables: wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index.	8	0.277	2034	0
H <sub>2</sub> . Individuals attending the colony.	3	0.046	8986	0
H <sub>3</sub> . Individuals attending the nests.	3	0.043	9049	0
<b>H<sub>4</sub>. Environmental variables and individuals attending the colony.</b>	10	0.346	0	1
H <sub>5</sub> . Environmental variables and individuals attending the nests.	10	0.329	331	1.3 e-72
H <sub>6</sub> . Null model.	3	0.014	9713	0

### 3.1.2. Individuals attending the colony

Regarding individuals attending the colony, the model that best explains this response variable (71% explanatory power) include environmental variables along with individuals attending both the colony and the nests (best model – H<sub>7</sub>) (Table 6). In this case, individuals attending the nests (H<sub>3</sub>) presented greater influence on the response variable (64.6%), along with environmental variables (H<sub>1</sub> – 41.9%). On the other hand, individuals attending the Berlenga Island (H<sub>2</sub>) appeared to have a residual influence on birds returning at the colony level (3.8%). Considering the model selected (H<sub>7</sub>), the response variable was positively influenced by individuals attending the island (0.001), individuals attending the nests (0.044), wave height (0.424), wave period (0.028) and upwelling index (0.0003) and negatively influenced by wind speed (-0.038), temperature (-0.092), precipitation (-3.733) and cloud cover (-0.017).

Table 6 Results of information-theoretic-based model selection for Cory's shearwaters returning to the Melreu colony: the number of model parameters (K), Nagelkerke's R<sup>2</sup> (R<sup>2</sup>), AIC<sub>c</sub> difference (Di) and Akaike weights (w<sub>i</sub>). In bold, the best competing model to explain the response variable.

Individuals attending the Melreu colony				
Hypothesis	K	R <sup>2</sup> adj	Di	w <sub>i</sub>
H <sub>1</sub> . Environmental variables: wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index.	8	0.419	655	5.9e-143
H <sub>2</sub> . Individuals attending the Berlenga island.	3	0.038	1702	0
H <sub>3</sub> . Individuals attending the nests.	3	0.646	260	3.3e-57
H <sub>4</sub> . Individuals attending the Berlenga Island and the nests.	4	0.640	257	1.6e-56
H <sub>5</sub> . Environmental variables and individuals attending the Berlenga Island.	10	0.459	518	4.0e-113
H <sub>6</sub> . Environmental variables and individuals attending the nests.	10	0.697	43	5.6e-10
<b>H<sub>7</sub>. Environmental variables and individuals attending the Berlenga Island and the nests.</b>	<b>11</b>	<b>0.711</b>	<b>0</b>	<b>1</b>
H <sub>8</sub> . Null model.	3	-0.015	1829	0

### 3.1.3. Individuals attending the nests

The hypothesis test showed that the number of individuals attending the nests was best explained (63% explanatory power) by environmental variables along with individuals attending both the island and the colony (best model – H<sub>7</sub>) (Table 7). Environmental variables (H<sub>1</sub>) and individuals attending the colony (H<sub>3</sub>) presented greater influences on the response variable (46.7% and 46.7%, respectively), contrarily to individuals attending the island (H<sub>2</sub>) that appeared to have a residual influence on the response variable (2.7%). Considering the model selected (H<sub>7</sub>), the

response variable was positively influenced by individuals attending the colony (0.015), wind speed (0.025), temperature (0.122), upwelling index (0.0002) and cloud cover (0.10) and negatively influenced by individuals attending the island ( $-3.951 \times 10^{-4}$ ), wave height (-0.907), wave period (-0.086) and precipitation (-3.270).

Table 7 Results of information-theoretic-based model selection for Cory's shearwaters returning to the Melreu nests: the number of model parameters (K), Nagelkerke's  $R^2$  ( $R^2_{adj}$ ),  $AIC_c$  difference (Di) and Akaike weights ( $w_i$ ). In bold, the best competing model to explain the response variable.

<b>Individuals attending the Melreu nests</b>				
<b>Hypothesis</b>	<b>K</b>	<b>R<sup>2</sup>adj</b>	<b>Di</b>	<b>w<sub>i</sub></b>
H <sub>1</sub> . Environmental variables: wind speed, wave height, wave period, temperature, precipitation, cloud cover and upwelling index.	8	0.467	192	1.57e-42
H <sub>2</sub> . Individuals attending the Berlenga Island.	3	0.027	759	1.21e-165
H <sub>3</sub> . Individuals attending the colony.	3	0.467	251	2.82e-55
H <sub>4</sub> . Individuals attending the Berlenga Island and the colony.	4	0.455	253	1.21e-55
H <sub>5</sub> . Environmental variables and individuals attending the Berlenga Island.	10	0.463	173	2.63e-38
H <sub>6</sub> . Environmental variables and individuals attending the colony.	10	0.633	7	2.82e-2
<b>H<sub>7</sub>. Environmental variables and individuals attending the Berlenga Island and the colony.</b>	<b>11</b>	<b>0.633</b>	<b>0</b>	<b>9.72e-1</b>
H <sub>8</sub> . Null model.	3	-0.017	810	1.18e-176

## 3.2. Distribution patterns and individual foraging behaviour

### 3.2.1. Pattern-Oriented Modelling

The Cory's shearwaters' habitat suitability in the vicinities of Corvo Island is displayed in Figure 6. The thresholds used to identify suitable feeding patches for the species during August 2010 were 0.06 mg m<sup>-3</sup> of chlorophyll-a (mg m<sup>-3</sup>), 23.6 °C of sea surface temperature and 730 m of bathymetry (Ceia et al., 2015). Real metrics of the Cory's shearwaters spatial distribution, obtained from tracked individuals in August 2010 at the Corvo Island (Ceia et al., 2015), are presented in Table 8.

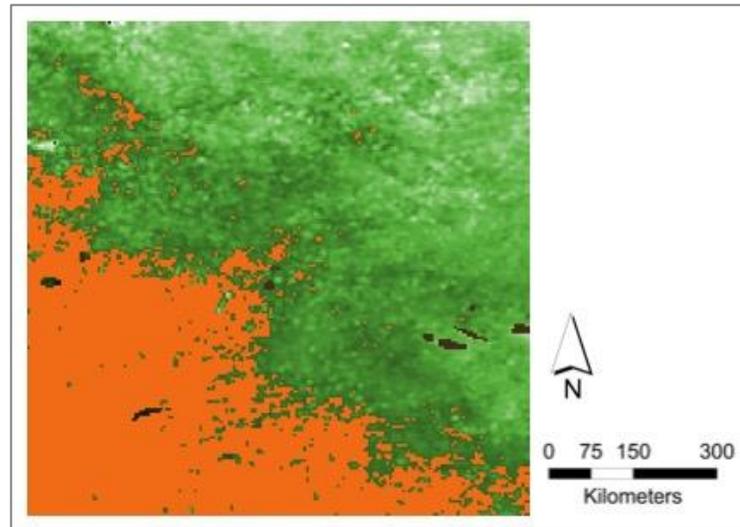


Figure 6 Cory's shearwaters habitat suitability around the Corvo Island during August 2010. Feeding areas are represented in orange and islands in brown. The thresholds used to identify suitable feeding patches for the species were  $0.06 \text{ mg m}^{-3}$  of chlorophyll-a ( $\text{mg m}^{-3}$ ),  $23.6 \text{ }^\circ\text{C}$  of sea surface temperature and 730 m of bathymetry. The background, in green, illustrates sea surface temperature ranging from  $23.4\text{ }^\circ\text{C}$  to  $28.3 \text{ }^\circ\text{C}$  (darker shades represent higher sea surface temperature).

Table 8 Data tracking from Ceia et al. (2015), used as baseline for comparison of simulated data. Values are presented as mean  $\pm$  standard deviation, discriminated for sub-colony A and sub-colony B. The metrics are: maximum distance from colony (Max-dist), mean distance from colony (Mean-dist), mean bearing from the colony to the most distant foraging locations (Mean-bearing), mean latitude position of foraging areas (Lat ARS zones), and mean longitude position of foraging areas (Long ARS zones). Fixed kernel density (75% FKD, 50% FKD and 25% FKD) correspond to the individual mean density contour areas.

	Data tracking (Ceia et al., 2015)							
	Max-dist (km)	Mean-dist (km)	75% FKD ( $\text{km}^2$ )	50% FKD ( $\text{km}^2$ )	25% FKD ( $\text{km}^2$ )	Mean-bearing	Lat ARS zones ( $^\circ \text{W}$ )	Long ARS zones ( $^\circ \text{N}$ )
Colony A	216	$62 \pm 39$	$158 \pm 63$	$61 \pm 32$	$23 \pm 14$	$84.4 \pm 38$	$39.8 \pm 0.4$	$-30.8 \pm 0.4$
Colony B			$135 \pm 68$	$53 \pm 25$	$19 \pm 8$	$251.2 \pm 52.5$	$39.8 \pm 0.4$	$-31.0 \pm 0.4$

The results obtained from simulated data revealed that virtual individuals tend to be more restrictive in using space around the breeding colony as foraging mechanisms were incorporated in simulations, namely in what concern to maximum distance travelled, mean foraging distance and mean density contour areas (Figure 7 and Table 9). Additionally, there is an apparently more obvious longitudinal segregation when virtual birds track olfactory and visual cues (Figure 7), with individuals from sub-colony A choosing to forage towards the eastern area of the Corvo Island and individuals from sub-colony B choosing to forage towards the western area of the Corvo Island. This pattern is supported by greater differences in mean bearing towards foraging areas between sub-colony A and

B, according to the olfactory-search with vision (Table 9). Furthermore, it is predicted an increase in mean-energy per virtual individual as long as foraging mechanisms become more complex (Table 9).

When comparing simulation results with real patterns obtained from Ceia et al. (2015), it seems that the CRW captures in a realistic way the spatial distribution of real tracked birds (Fig. 7), with greater differences becoming apparent as long as foraging mechanisms are incorporated in the simulations. Nevertheless, this pattern is not corroborated by the quantitative metrics obtained, in which comparisons with real density contour areas (Table 9) point to a more realistic performance of the olfactory-search with vision at the individual level of space use (FKD 25, 50 and 75%) (Table 9).

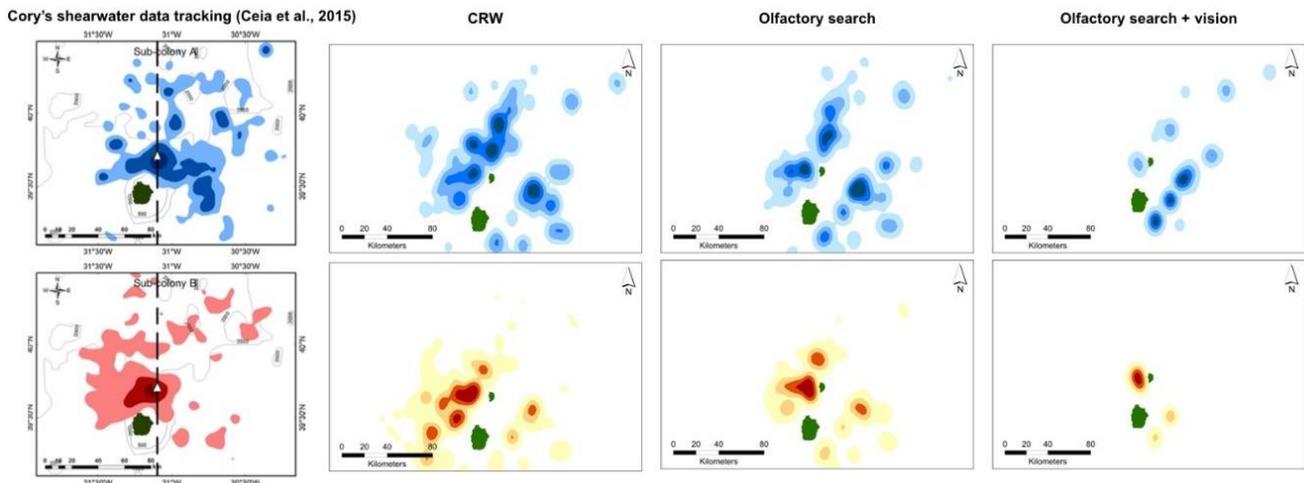


Figure 7 Real and simulated spatial distribution of Cory's shearwaters from sub-colonies A (blue) and B (red), during August 2010 in the vicinities of Corvo Island: left panel (Cory's shearwaters data tracking) - 25, 50 and 75 % density contour areas calculated by fixed kernel density, obtained from Ceia et al. (2015); right panels (CRW, Olfactory search and Olfactory search + vision) - 25, 50, 75 and 100 % density contour areas calculated by fixed kernel density, obtained from simulation results . The colour gradient, from darker to lighter shades represent 25, 50, 75% and home range (100%) kernel densities, respectively.

Table 9 Cory's shearwater simulated data for sub-colony A and sub-colony B, considering different foraging mechanisms (CRW, olfactory-search and olfactory-search with vision). The metrics are: maximum distance from colony (Max-dist), mean distance from colony (Mean-dist), mean bearing from the colony to the most distant foraging locations (Mean-bearing), mean latitude position of foraging areas (Lat ARS zones), mean longitude position of foraging areas (Long ARS zones) and mean energy obtained per individual in the end of a foraging day (Mean-energy per individual). Fixed kernel density (75% FKD, 50% FKD and 25% FKD) correspond to the individual mean density contour areas. Values are presented as mean  $\pm$  standard deviation, discriminated for sub-colony A and sub-colony B.

	Static environmental					
	CRW		Olfactory-search		Olfactory-search + vision	
	Sub-colony A	Sub-colony B	Sub-colony A	Sub-colony B	Sub-colony A	Sub-colony B
<b>Max-dist (km)</b>	321		318		307	
<b>Mean-dist (km)</b>	96 $\pm$ 87.0		54.2 $\pm$ 63.8		27.4 $\pm$ 28.8	
<b>75% FKD (km<sup>2</sup>)</b>	1424.6 $\pm$ 795.4	877.6 $\pm$ 642.7	937.4 $\pm$ 444.8	676.3 $\pm$ 608.9	360 $\pm$ 223.0	188 $\pm$ 30.0
<b>50% FKD (km<sup>2</sup>)</b>	570.4 $\pm$ 339.2	325.2 $\pm$ 269	327 $\pm$ 177.9	224.4 $\pm$ 45.4	134 $\pm$ 63.1	88.3 $\pm$ 8.3
<b>25% FKD (km<sup>2</sup>)</b>	174.8 $\pm$ 115.8	103.1 $\pm$ 81	100.2 $\pm$ 53.2	71.3 $\pm$ 44.8	47.5 $\pm$ 16.9	35.8 $\pm$ 3.0
<b>Mean-bearing</b>	117.5 $\pm$ 87.5	176 $\pm$ 100	115.8 $\pm$ 66.3	170.3 $\pm$ 59	116.5 $\pm$ 43.5	190 $\pm$ 65.9
<b>Lat ARS zones (° N)</b>	39.6 $\pm$ 0.8	39.6 $\pm$ 0.3	39.6 $\pm$ 0.4	39.6 $\pm$ 0.4	39.6 $\pm$ 0.2	39.6 $\pm$ 0.1
<b>Long ARS zones (° W)</b>	-31.0 $\pm$ 0.5	-31.3 $\pm$ 0.3	-30.9 $\pm$ 0.3	-31.1 $\pm$ 0.2	-30.9 $\pm$ 0.2	-31.1 $\pm$ 0.1
<b>Mean-energy per individual</b>	32.7 $\pm$ 0.4	85.3 $\pm$ 0.3	70.5 $\pm$ 32	98.5 $\pm$ 21	94.8 $\pm$ 16.6	112 $\pm$ 9.0

### 3.2.2. Influence of foraging mechanisms, density of foraging individuals and resources distribution in the Cory's shearwater Individual foraging efficiency

The three hypothetical scenarios regarding abundant, intermediate and scarce resources distribution around the Corvo island are presented in Figure 8. The tested abundances of virtual birds for the simulated colony were 100, 500 and 2000 individuals.

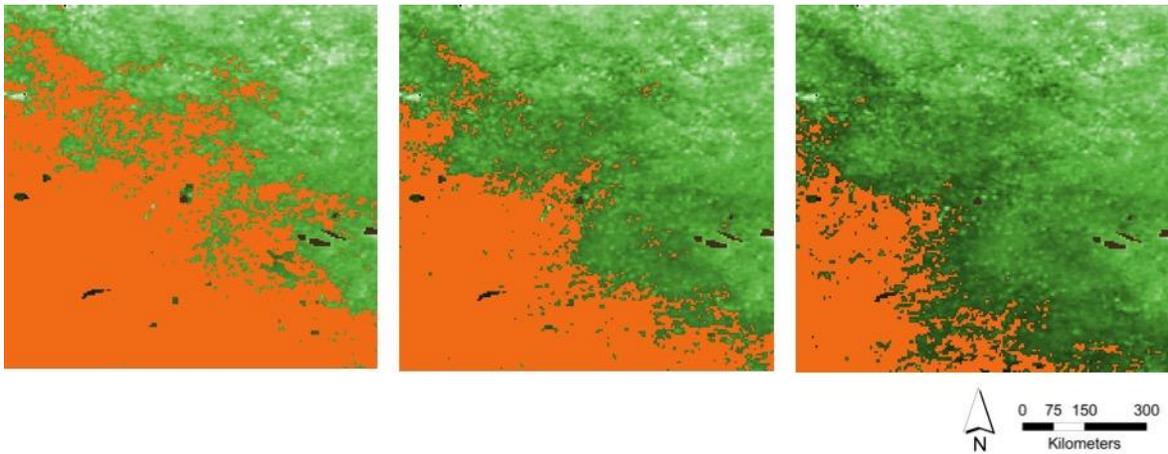


Figure 8 Cory's shearwaters habitat suitability around the Corvo Island in 3 hypothetical scenarios; (left) abundant resources distribution ( $0.05 \text{ mg m}^{-3}$  of chlorophyll-*a*,  $23.0 \text{ }^{\circ}\text{C}$  of sea surface temperature and  $720 \text{ m}$  of bathymetry); (middle) intermediate resources distribution ( $0.06 \text{ mg m}^{-3}$  of chlorophyll-*a*,  $23.5 \text{ }^{\circ}\text{C}$  of sea surface temperature and  $730 \text{ m}$  of bathymetry); (right) scarce resources distribution ( $0.07 \text{ mg m}^{-3}$  of chlorophyll-*a*,  $24.0 \text{ }^{\circ}\text{C}$  of sea surface temperature and  $740 \text{ m}$  of bathymetry). Feeding areas are represented in orange and islands in brown. The background, in green, illustrates sea surface temperature ranging from  $23.4^{\circ}\text{C}$  to  $28.3 \text{ }^{\circ}\text{C}$  (darker shades represent higher sea surface temperature).

For all scenarios, the obtained results indicate significant differences in foraging efficiency of virtual individuals between the different foraging mechanisms considered. Additionally, increasing in mean energy obtained per virtual individual was observed as foraging mechanisms become more complex, for all abundances considered (Table 10, 11 and 12).

Table 10 Differences in the foraging efficiency of individuals (mean energy per individual) taking into account different foraging mechanisms (correlated random walk (crw), olfactory search (olf) and olfactory search with vision (olf + vis)), in the scenario of abundant resources around the breeding colony. Significant differences are signed in bold.

	Abundant resources – foraging mechanism influence						
	Kruskal-Wallis test				Dunn test		
	median (crw)	median (olf)	median (olf+v)	p-value	crw / olf	crw / olf+v	olf / olf+v
<b>100</b>	100.36	110.57	112.49	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>500</b>	100.12	110.4	112.92	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>2000</b>	99.93	110.48	113.21	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>

Table 11 Differences in the foraging efficiency of individuals (mean energy per individual) taking into account different foraging mechanisms (correlated random walk (crw), olfactory search (olf) and olfactory search with vision (olf + vis)), in the scenario of intermediate resources around the breeding colony. Significant differences are signed in bold.

Intermediate resources – foraging mechanism influence							
	Kruskal-Wallis test				Dunn test		
	median (crw)	median (olf)	median (olf+v)	p-value	crw / olf	crw / olf+v	olf / olf+v
<b>100</b>	88.89	101.61	105.93	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>500</b>	89.05	101.45	107.29	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>2000</b>	89.07	101.28	108.08	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>

Table 12 Differences in the foraging efficiency of individuals (mean energy per individual) taking into account different foraging mechanisms (correlated random walk (crw), olfactory search (olf) and olfactory search with vision (olf + vis)), in the scenario of scarce resources around the breeding colony. Significant differences are signed in bold.

Scarce resources – foraging mechanism influence							
	Kruskal-Wallis test				Dunn test		
	median (crw)	median (olf)	median (olf+v)	p-value	crw / olf	crw / olf+v	olf / olf+v
<b>100</b>	16.15	19.94	22.94	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>500</b>	16.01	20.23	25.01	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>2000</b>	15.99	19.98	26.51	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>

Regarding the influence of the number of virtual foraging individuals, significant differences in foraging efficiency were restricted to the olfactory-search with vision, in all scenarios and abundances of birds considered (Table 13, 14 and 15). Furthermore, the abundance of virtual foraging individuals significantly improved the individual foraging efficiency, with an increase in mean energy per virtual individual as more birds forage in the same area, for all scenarios. Greater differences were found when resources are scarce around breeding colonies (Table 13, 14 and 15). Differences were also found for the olfactory search under the scenario of intermediate resources, although in the threshold of significance (Table 14).

Table 13 Differences in the foraging efficiency of individuals (mean energy per individual) taking into account different abundances of foraging individuals (100, 500 and 2000 individuals) and foraging mechanisms (correlated random walk (CRW), olfactory search and olfactory search (Olfactory) with vision (olfactory + vis)), in the scenario of abundant resources around the breeding colony. Significant differences are signed in bold.

	Abundant resources – individuals influence						
	Kruskal-Wallis test				Dunn test		
	median (100 ind)	median (500 ind)	median (2000 ind)	p-value	100 / 500	100 / 2000	500 / 2000
<b>CRW</b>	100.36	100.12	99.93	0.2526	0.2975	0.0519	0.1367
<b>Olfactory search</b>	110.57	110.4	110.48	0.2112	0.0556	0.4439	0.0733
<b>Olfactory + vision</b>	112.49	112.92	113.21	<b>0</b>	<b>0.0005</b>	<b>0</b>	<b>0</b>

Table 14 Differences in the foraging efficiency of individuals (mean energy per individual) taking into account different abundances of foraging individuals (100, 500 and 2000 individuals) and foraging mechanisms (correlated random walk (CRW), olfactory search and olfactory search (Olfactory) with vision (olfactory + vis)), in the scenario of intermediate resources around the breeding colony. Significant differences are signed in bold.

	Intermediate resources – individuals influence						
	Kruskal-Wallis test				Dunn test		
	median (100 ind)	median (500 ind)	median (2000 ind)	p-value	100 / 500	100 / 2000	500 / 2000
<b>CRW</b>	88.89	89.05	89.07	0.7791	0.2797	0.2622	0.4789
<b>Olfactory search</b>	101.61	101.45	101.28	<b>0.04654</b>	0.2233	<b>0.0077</b>	<b>0.0484</b>
<b>Olfactory + vision</b>	105.93	107.29	108.08	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>

Table 15 Differences in the foraging efficiency of individuals (mean energy per individual) taking into account different abundances of foraging individuals (100, 500 and 2000 individuals) and foraging mechanisms (correlated random walk (CRW), olfactory search and olfactory search (Olfactory) with vision (olfactory + vis)), in the scenario of scarce resources around the breeding colony. Significant differences are signed in bold.

	Scarce resources – individuals influence						
	Kruskal-Wallis test				Dunn test		
	median (100 ind)	median (500 ind)	median (2000 ind)	p-value	100 / 500	100 / 2000	500 / 2000
<b>CRW</b>	16.15	16.01	15.99	0.8687	0.3413	0.4648	0.3095
<b>Olfactory</b>	19.94	20.23	19.98	0.712	0.2077	0.3832	0.3025
<b>Olfactory + vision</b>	22.94	25.01	26.51	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>

## 4. DISCUSSION

1. How do environmental conditions influence the returning of individuals to the island, colony and nests?

According to our results, the returning of Cory's shearwaters at the Berlenga Island, the Melreu colony and respective nests seemed to be highly influenced by the environmental conditions around the Berlenga Island, with larger effects at the colony and nests levels. In fact, during reproduction, seabirds act as central-place foragers, preferentially foraging in the vicinities of the breeding colonies, at local continental/oceanic shelves and/or neighbouring pelagic/neritic waters, either to minimize incubation shifts length or to maximize offspring provisioning rates (Paiva et al., 2010; Weimerskirch et al., 1994). In this context, since the Berlenga Island is located in a neritic system that supplies profitable foraging grounds for seabirds (Paiva et al., 2010b; Paiva et al., 2010), the environmental variables included in this study may be acting as proxies of resources availability and consequently individual foraging success. This could also partially explain the returning of individuals to nesting sites (Granadeiro et al., 2009). On the other hand, in oceanic colonies, cycles of colony attendance did not seem to be driven by environmental factors, such as oscillations in food availability or accessibility around breeding colonies, partially explained by individual physiological trade-offs between investing in reproduction or ensuring own survival (Granadeiro et al., 2009). Furthermore, the decreased explanatory power of environmental variables explaining the returning of birds to the island (~30%), when compared with the returning of birds to the colony (~42%) and nests (~47), may be related with other processes acting at coarse scales, such as behavioural mechanisms acting among individuals from neighbouring colonies.

2. To what extent density-dependent mechanisms are related with the returning of individuals to the island, the colony and the nests?

According to our results, density-dependent mechanisms seem to occur with higher expression at the colony and nests levels, with a residual influence verified at the Berlenga Island. In fact, social interactions have been demonstrated as important factors shaping seabirds' foraging behaviour through network foraging (Weimerskirch et al., 2010). In this context, the return of individuals to the colony seems to positively influence the returning of individuals to the nests, and vice versa, which may be in line with intra-colony cooperation mechanisms promoting social encounters that are essential for information transfer between conspecifics (Boyd et al., 2016). Furthermore, Granadeiro et al. (2009) also supports the idea that synchronization among individuals at the colony level may be influenced by local processes, such as social interactions, through which birds increase the likelihood of meeting relevant social contacts at the colony, such as partners and competitors for nesting sites (social encounters hypothesis, Mougín et al., 2000).

Additionally, the residual correlation between birds attending the island and birds attending the colony or nests may underlie the existence of cooperation mechanisms acting at the sub-colonies level. In fact, segregation may work as a mechanism to reduce inter-colony competition, allowing proximate colonies to co-exist in the same geographical area without overlapping main feeding areas in time and/or space (Paiva, Xavier, Geraldés, Ramirez, et al., 2010; Wiley et al., 2012); a pattern also described in Cory's shearwaters (Ceia et al., 2015). Nevertheless, the partial overlap of potential foraging areas among individuals from different sub-colonies (Ceia et al., 2015) may also indicate advantages in information transfer between conspecifics from different sub-colonies. Therefore, to fully understand birds' attendance at the island level, more data is needed to explore the role of competition/cooperation mechanisms acting among individuals from different sub-colonies established in the same Island.

3. To what extent the use of different foraging mechanisms may affect the Cory's shearwater distribution patterns and habitat usage?

The Pattern Oriented Modelling approach allowed to evaluate which foraging decision rules (Correlated Random Walk, olfactory-search or olfactory-search with vision) caused the IBM model to best reproduce a range of patterns observed in real tracked individuals from Corvo island during August 2010 (Ceia et al., 2015). When comparing simulation results with real patterns obtained from Ceia et al. (2015), the CRW, in which the step length and the turning angle followed the distribution of real Cory's shearwater movement behaviours (ARS and travel), was able to capture in a realistic way the spatial distribution and space use of tracked birds at the sub-colonies level (Bergman et al., 2000; Morales et al., 2004). Nevertheless, although greater visual differences seemed to occur between real and simulated patterns with the inclusion of additional foraging mechanisms (Figure 7), mean density contour areas point to a more realistic performance of the olfactory-search with vision in reproducing spatial patterns of habitat use at the individual level (FKD 25, 50 and 75%) (Table 8 versus Table 9). In fact, our results show that individuals tend to be more restrictive in using space around the breeding colony, namely in what concern to maximum distance travelled, mean foraging distance and mean density contour areas, leading to a more efficient resource use as foraging mechanisms become more complex (including a predicted increase in mean-energy obtained per individual). Additionally, since longitudinal segregation becomes more pronounced as virtual birds were able to track visual cues, we support the idea that this directional tendency may be reinforced by information transfer between foragers (Ward & Zahavi, 1973). Finally, since the olfactory search and olfactory search with vision is a combined approach that includes the geometric characteristics of the animal movements biased towards the landscape characteristics and social interactions with conspecifics, the obtained differences in spatial patterns may be related with the lack of incorporation of additional foraging mechanisms, such as social learning through rafts and personal learning through memory, which are likely to drive a wide spatial distribution of individuals at the sub-colonies level.

4. How does the use of olfactory search and social information transfer (local enhancement) may affect the feeding efficiency of individuals foraging in different environmental conditions?

For all scenarios and densities of foraging individuals tested, our results point to a significant increase in mean energy gain per individual as foraging mechanisms become more complex, highlighting a relative increase in the individuals' average intake in the scenario of scarce resources distribution around breeding colonies. In this context, it is expected that more sophisticated mechanisms may allow individuals to acquire more information, either through olfactory and/or network foraging strategies (Boyd et al., 2016; Nevitt et al., 2008). This information might contribute to an increase in individuals' foraging success (Weimerskirch et al., 2010) especially when resources are scarce around breeding colonies. On the other hand, under abundant resources distribution around nesting sites, complex mechanisms appear to have a relative lower effectiveness on individual foraging success, since individuals may encounter food resources easily.

5. What is the interplay between the density of foraging individuals and the effectivity of local enhancement in different scenarios of resources abundance and distribution around breeding colonies?

Our results are in accordance with the local enhancement hypothesis (Buckley, 1997; Mock et al., 1988), suggesting that the mechanisms underpinning local enhancement are more effective under increasing population densities (Boyd et al., 2016), namely by improving the probability of encounters with successful feeders (Thiebault et al., 2014). Furthermore, greater differences in individual mean energy intake were found when resources are scarce around breeding colonies, indicating that birds foraging in poorer conditions may be more dependent on conspecifics to find unpredictable distributed food patches (Boyd et al., 2016) than birds breeding in more profitable areas. In this context, Granadeiro et al. (2009) proposed that attendance cycles are more likely to occur where large numbers of birds are simultaneously present. We stress the importance of cooperation mechanisms through social network in promoting individual foraging success and consequently driving the returning of individuals to nesting sites. We argue that this can be especially important for colonies established in poorer conditions.

### **Future research perspectives**

With this work, we intended to explore the role of environmental factors, density-dependent and foraging mechanisms driving the Cory's shearwater foraging behaviour and distribution. The POM approach allowed us to balance the strengths and fragilities of the IBM' conceptualization, from which future research perspectives should be directed to the inclusion of additional foraging mechanisms, namely social learning through rafts and personal learning through

memory. In fact, the coexistence of different foraging mechanisms in the same species is likely to occur (Barta & Giraldeau, 2001). For example, in murre, compass rafts are probably used when patches are unpredictable (Burger, 1997) but memory and local enhancement are used when prey location is predictable and reliable over longer periods of time (Davoren et al., 2003). Additionally, it would be interesting to explore dynamic scenarios in order to investigate the role of spatio-temporal environmental variability in the foraging behaviour and spatial patterns obtained. An approach following the unified foraging theory (Mangel & Clark, 1986) based on trade-offs between expenses and benefits of movements, such as provisioning behaviour and survival, could also give important insights about the selection of some habitats and the adaptive behaviour of Cory's shearwaters to spatio-temporal variability in resources availability.

Therefore, future research questions that emerge from this study are:

- How the use of personal information (memory) and social information (local enhancement + rafts) may affect the feeding efficiency of individuals foraging in different environmental conditions?
- How do resource availability can shape the employment of different searching mechanisms during foraging?
- To what extent individuals adapt foraging strategies taking into account the spatio-temporal variability of resource location around breeding colonies?

### **Future research applications**

At a time when the Earth's sixth mass extinction is discussed among researches (Barnosky et al., 2011), primary production is in decline (Behrenfeld et al., 2006) and we are witnessing a global climate change (Grémillet & Boulinier, 2009; United Nations, 2016), it is crucial to assess the influence of environmental changing conditions in the adaptive foraging behaviour of top predators. In fact, seabirds' behavioural characteristics might constrain their adaptation to such changes since many birds display considerable breeding site philopatry, sometimes remaining faithful to an area even after conditions have become unfavourable (Grémillet et al., 2008). Therefore, the behavioural, social and life-history traits of seabirds may render them particularly sensitive to climate change (Grémillet & Boulinier, 2009). In this context, the identification of pelagic hotspots and its characterization taking into account future changes in marine ecosystems is required to support the conservation of top predators (Lewison et al., 2012) and suggest networks of priority marine conservation areas (Maxwell et al., 2015).

## **5. CONCLUSIONS**

This work demonstrated that Cory's shearwater attendance patterns in the Berlenga Island are influenced by environmental conditions and density-dependent mechanisms, acting with higher influence at local scales. Additionally, our study shows that an olfactory search combined with information transfer between conspecifics tend to be the most reliable foraging strategy in reproducing the Cory's shearwater spatial patterns at the individual level. In this context, more complex foraging mechanisms seem to promote individual foraging efficiency, where increasing population densities improve the effectiveness of network foraging through local enhancement, especially in scenarios where resources are scarce around breeding colonies. Finally, through the discussion of the results attained raise the question if the density-dependent mechanisms associated with foraging behaviour and effectiveness of social foraging may somehow underpin patterns of individuals' attendance at nesting colonies. However, more research is needed to confirm this hypothesis. In conclusion, the statistical approach used in this study proved to be a valuable tool in testing ecological hypothesis for the explanation of the Cory's shearwater attendance patterns, whereas the IBM approach allowed to better understand the processes and mechanisms involved in the Cory's shearwater foraging behaviour and spatial distribution, including how individuals are likely to perceive and adapt to their environment.

## 6. REFERENCES

- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G., Swartz, B., Quental, T. B., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471* (7336), 51-57. <http://doi.org/10.1038/nature09678>
- Barta, Z., & Giraldeau, L. (2001). Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer-scrourer game. *Behavioral Ecology*, *12* (2), 121-127. <http://doi.org/10.1093/beheco/12.2.121>
- Bastos, R., D'Amen, M., Vicente, J., Santos, M., Yu, H., Eitelberg, D., et al. (2016). A multi-scale looping approach to predict spatially dynamic patterns of functional species richness in changing landscapes. *Ecological Indicators*, *64*, 92–104.
- Bastos, R., Santos, M., Ramos, J. A., Vicente, J., Guerra, C., Alonso, J., et al. (2012). Testing a novel spatially-explicit dynamic modelling approach in the scope of the laurel forest management for the endangered Azores bullfinch (*Pyrrhula murina*) conservation. *Biological Conservation*, *147*(1), 243–254.
- Behrenfeld, M. J., O'Malley, R. T., Siegel, D. a, McClain, C. R., Sarmiento, J. L., Feldman, G. C., et al. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, *444*(7120), 752–755.
- Bergman, C. M., Schaefer, J., & Luttich, S. N. (2000). Caribou movement as a correlated random walk. *Oecologia*, *123* (3), 364-374. <http://doi.org/10.1007/s004420051023>
- Berryman, M. J., & Angus, S. D. (2010). Tutorials on Agent-based Modelling with NetLogo and Network Analysis with Pajek. *Complex Physical, Biophysical and Econophysical Systems - Proceedings of the 22nd Canberra International Physics Summer School*, 351-375. [http://doi.org/10.1142/9789814277327\\_0010](http://doi.org/10.1142/9789814277327_0010)
- BirdLife International. (2017). *Calonectris borealis*. *The IUCN Red List of Threatened Species 2017*.
- Boyd, C., Grünbaum, D., Hunt, G. L., Punt, A. D., Weimerskirch, H., & Bertrand, S. (2016). Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. *Behavioral Ecology*, *27*(4), 1223–1234.
- Buckley, N. J. (1997). Spatial-concentration effects and the importance of local enhancement in the evolution of colonial breeding in seabirds. *The American Naturalist*, *149* (6), 1091-1112. <http://doi.org/10.1086/286040>
- Burger, A. E. (1997). Arrival and departure behavior of common murrelets at colonies: evidence for an information halo? *Colonial Waterbirds*, *20* (1), 55-65. <http://doi.org/10.2307/1521764>
- Burke, C. M., & Montevecchi, W. A. (2009). The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology*, *278* (4), 354-361. <http://doi.org/10.1111/j.1469-7998.2009.00584.x>
- Burnham, K., & Anderson, D. (2002). *Model Selection and Multi-Model Inference*. San Francisco, CA, *itd: Morgan Kaufmann*. [http://doi.org/10.1002/1521-3773\(20010316\)40:6<9823::AID-ANIE9823>3.3.CO;2-C](http://doi.org/10.1002/1521-3773(20010316)40:6<9823::AID-ANIE9823>3.3.CO;2-C)
- Calenge, C. (2006). The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 516-519. <http://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Ceia, F. R., Paiva, V. H., Ceia, R. S., Hervías, S., Garthe, S., Marques, J. C., & Ramos, J. A. (2015). Spatial foraging segregation by close neighbours in a wide-ranging seabird. *Oecologia*, *177*(2), 431–440.
- Danchin, E., Giraldeau, L., Valone, T., Wagner, R. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, *305* (5683), 487–491. <http://doi.org/10.1126/science.1098254>
- Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003). Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecological Monographs*, *73* (3), 463-481. <http://doi.org/10.1890/02-0208>
- DeAngelis, D. L., & Mooij, W. M. (2005). Individual-based Modeling of Ecological and Evolutionary Processes. *Annual Review of Ecological and Evolutionary Systems*, *36* (1), 147-168. <http://doi.org/10.1>

- Elith, J., Graham, C., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. doi:10.1111/j.2006.0906-7590.04596.x
- Fauchald, P. (1999). Foraging in a Hierarchical Patch System. *The American Naturalist*, 153 (6), 603-613. <http://doi.org/10.1086/303203>
- Fauchald, P., & Tveraa, T. (2003). Using first-passage time in the analysis of area restricted search and habitat selection. *Ecology*, 84 (2), 282-288. [http://doi.org/10.1890/0012-9658\(2003\)084\[0282:UFPTIT\]2.0.CO;2](http://doi.org/10.1890/0012-9658(2003)084[0282:UFPTIT]2.0.CO;2)
- Granadeiro, J. P., Alonso, H., Almada, V., Menezes, D., Phillips, R. A., & Catry, P. (2009). Mysterious attendance cycles in Cory's shearwater, *Calonectris diomedea*: an exploration of patterns and hypotheses. *Animal Behaviour*, 78(6), 1455–1462.
- Grémillet, D., & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: A review. *Marine Ecology Progress Series*, 391, 121-137.
- Grémillet, D., Lewis, S., Drapeau, L., Van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., et al. (2008). Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, 45 (2), 610-621. <http://doi.org/10.1111/j.1365-2664.2007.01447.x>
- Grimm, V., & Railsback, S. (2005). Individual-based modeling and ecology. *Individual-Based Modeling and Ecology*, 1-432. <http://doi.org/10.1111/j.1467-2979.2008.00286.x>
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modeling*, 135, 147-186.
- Instituto da Conservação da Natureza e das Florestas. (n.d.). Reserva da Biosfera - Berlengas (mapa), from <http://www.icnf.pt/portal/pn/biodiversidade/ei/resource/img/mab/rb-berleng-map/view>
- Lalli, C. M., & Parsons, T. R. (1997). *Biological Oceanography - An Introduction* (2nd ed.). Oxford: Elsevier Butterworth-Heinemann.
- Lecoq, M. (2010). *Censo da população reproductora da cagarra na ilha da Berlenga em 2010*. Relatório de acção A - Actividade 2. Projecto FAME. Sociedade Portuguesa para o Estudo das Aves, Lisboa (relatório não publicado).
- Lecoq, M., Gerales, P., & Andrade, J. (2011). First complete census of Cory's Shearwaters *Calonectris diomedea borealis* breeding at Berlengas Islands (Portugal), including the small islets of the archipelago. *Airo*, 21 (June), 31-34.
- Lewison, R., Oro, D., Godley, B. J., Underhill, L., Bearhop, S., Wilson, R. P., et al. (2012). Research priorities for seabirds: Improving conservation and management in the 21st century. *Endangered Species Research*, 17 (2), 93-121.
- Lynch, H. J., Thorson, J. T., & Shelton, A. O. (2014). Dealing with under- and over-dispersed count data in life history, spatial, and community ecology. *Ecology*, 95 (11), 3173-3180. <http://doi.org/10.1890/13-1912.1>
- Magalhães, M. C., Santos, R. S., & Hamer, K. C. (2008). Dual-foraging of Cory's shearwaters in the Azores: Feeding locations, behaviour at sea and implications for food provisioning of chicks. *Marine Ecology Progress Series*, 359, 283–293.
- Mangel, C., & Clarck, C. (1986). Towards a unified foraging theory. *Ecology*, 67(5), 1127–1138.
- Martin, G. R., & Brooke, M. (1991). The eye of a procellariiform seabird, the Manx shearwater, *Puffinus puffinus*: visual fields and optical structure. *Brain, Behavior and Evolution*, 37 (2), 65-78. <http://doi.org/10.1159/000114347>
- Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., et al. (2015). Dynamic ocean management: defining and conceptualizing real-time management of the ocean. *Marine Policy*, 58, 42-50. <http://doi.org/10.1016/j.marpol.2015.03.014>
- Mcmahon, B. J., Purvis, G., Sheridan, H., Siriwardena, G. M., & Parnell, A. C. (2016). A novel method for quantifying overdispersion in count data and its application to farmland birds. *Ibis*, 158, 406-414. <http://doi.org/doi:10.1111/ibi.12450>
- Mock, D. W., Lamey, T. C., & Thompson, D. B. (1988). Falsifiability and the information centre hypothesis. *Ornis Scandinavica*, 19 (3), 231-248. <http://doi.org/10.2307/3676564>

- Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology*, *85* (9), 2436-2445. <http://doi.org/10.1890/03-0269>
- Mougin, J. L., Jouanin, C., & Roux, F. (2000). The attendance cycles of the Cory's shearwater (*Calonectris diomedea borealis*) on Selvagem Grande. *Comptes Rendus de l'Academie Des Sciences - Serie III*, *323* (4), 385-390. [http://doi.org/10.1016/S0764-4469\(00\)00142-6](http://doi.org/10.1016/S0764-4469(00)00142-6)
- Neter, J., Kutner, M. H., Nachtsheim, C. J., & Wasserman, W. (1996). *Applied linear statistical models*. Irwin, Chicago.
- Nevitt, G. A., Losekoot, M., & Weimerskirch, H. (2008). Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences*, *105* (12), 4576-4581. <http://doi.org/10.1073/pnas.0709047105>
- Oppel, S., Hervias, S., Oliveira, N., Pipa, T., Silva, C., Geraldes, P., et al. (2014). Estimating population size of a nocturnal burrow-nesting seabird using acoustic monitoring and habitat mapping. *Nature Conservation*, *7*, 1-13. <http://doi.org/10.3897/natureconservation.7.6890>
- Paiva, V. H., Geraldes, P., Ramírez, I., Garthe, S., & Ramos, J. A. (2010). How area restricted search of a pelagic seabird changes while performing a dual foraging strategy. *Oikos*, *119*(9), 1423–1434.
- Paiva, V. H., Geraldes, P., Ramírez, I., Meirinho, A., Garthe, S., & Ramos, J. A. (2010a). Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Marine Ecology Progress Series*, *398*, 259–274.
- Paiva, V. H., Geraldes, P., Ramírez, I., Meirinho, A., Garthe, S., & Ramos, J. A. (2010b). Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. *Marine Biology*, *157*(6), 1385–1399.
- Paiva, V. H., Xavier, J., Geraldes, P., Ramirez, I., Garthe, S., & Ramos, J. A. (2010). Foraging ecology of Cory's shearwaters in different oceanic environments of the North Atlantic. *Marine Ecology Progress Series*, *410*, 257–268.
- R Core Team. (2017). *R: a language and environment for statistical computing*. Vienna, Austria. Accessed from: <https://www.r-project.org/>
- Railsback, S. F., & Johnson, M. D. (2011). Pattern-oriented modeling of bird foraging and pest control in coffee farms. *Ecological Modelling*, *222* (18), 3305-3319. <http://doi.org/10.1016/j.ecolmodel.2011.07.009>
- Shono, H. (2000). Efficiency of the finite correction of Akaike's Information Criteria. *Fisheries Science*, *66*(3), 608–610.
- Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, *25*(6), 1302–1310.
- Thiebault, A., Mullers, R., Pistorius, P., Meza-Torres, M. A., Dubroca, L., Green, D., & Tremblay, Y. (2014). From colony to first patch: processes of prey searching and social information in Cape Gannets. *Auk*, *131*(4), 595–609.
- United Nations. (2016). *The First Global Integrated Marine Assessment - World Ocean Assessment I*, from [http://www.un.org/depts/los/global\\_reporting/WOA\\_RPROC/Title\\_Page.pdf](http://www.un.org/depts/los/global_reporting/WOA_RPROC/Title_Page.pdf)
- Ver Hoef, J., & Boveng, P. (2007). Quasi-poisson vs. negative binomial regression: How should we model overdispersed data? *Ecology*, *88* (11), 2766-2772.
- Vicente, J., Alves, P., Randin, C., Guisan, A., & Honrado, J. (2010). What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. *Ecography*, *33* (6), 1081-1092. <http://doi.org/10.1111/j.1600-0587.2010.6380.x>
- Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of bird as "information centres" for food-findings. *Ibis*, *115* (4), 517-534. <http://doi.org/10.1111/j.1474-919X.1973.tb01990.x>
- Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 211–223.
- Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C., & Goya, E. (2010). Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLoS ONE*, *5*(3).

- Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeier, X., & Judas, J. (1994). Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour*, 472-476. <http://doi.org/10.1006/anbe.1994.1065>
- Wilensky, U. (1999). Netlogo. Accessed from: <https://ccl.northwestern.edu/netlogo/>
- Wiley, A. E., Welch, A. J., Ostrom, P. H., James, H. F., Stricker, C. A., Fleischer, R. C., et al. (2012). Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia*, 168 (1), 119-130. <http://doi.org/10.1007/s00442-011-2085-y>
- Wisz, M. S., & Guisan, A. (2009). Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecology*, 9, 8. <http://doi.org/10.1186/1472-6785-9-8>