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Foraging ecology of breeding shearwaters in the North Atlantic: A multi-level modelling approach to support upcoming decision-making for the conservation of marine ecosystems

Tese de Doutoramento em Ciência, Tecnologia e Gestão do Mar

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Abstract

Global warming is forcing persistent and unprecedented changes in the marine environment, imposing a major challenge to scientists, policy makers and environmental managers in finding solutions for the oceans future sustainability. Marine top predators, such as seabirds, are largely regulated by food web dynamics, offering unique insights into marine ecosystem status and change. Therefore, predicting seabird responses to variations in resources availability and anticipating their ability to cope with future environmental conditions can provide relevant supporting information for the management and conservation of marine species and habitats. In this thesis, I used GPS tracking datasets of Cory's and Cape Verde shearwaters (*Calonectris borealis* and *Calonectris edwardsii*, respectively) and mechanistic modelling approaches, such as system dynamics and agent-based models, to explore hypothesis related to the foraging ecology of shearwaters breeding in the North Atlantic Ocean (Berlengas, Azores, Madeira and Cape Verde archipelagos). In particular, I investigated individual-level mechanisms underlying shearwaters foraging behaviour during chick rearing , and evaluated behavioural strategies that enable individuals to maximize their fitness under contrasting foraging conditions. A special emphasis was given to processes related with their sensorial and cognitive capacities to locate prey at sea, and the need to balance the demands of self-feeding and chick provisioning within the constraints imposed by central place foraging. I also explored ecological imbalances triggered by human-induced environmental changes with consequences for the reproductive ecology of Cory's shearwaters through predatory pressures at breeding sites. This study revealed: 1) a potential link between shearwaters foraging behaviour and the decision processes associated with timing of nest arrival; 2) a synergistic effect between olfactory foraging and local enhancement for the optimal foraging behaviour of pelagic seabirds; 3) flexible strategies of parental behaviour and cooperation for chick provisioning and foraging decisions; and 4) guidelines for site-specific management programs with implications for the conservation of shearwaters. This thesis ends with the integration of these main findings into a modelling framework proposal that aims to use information about seabirds foraging behaviour and ecology into the conservation of marine ecosystems, including conceptual and technical advances for its future implementation using the Cory's shearwater as a target model species. Overall, this study advances understanding about the behavioural flexibility of shearwaters to variations in foraging conditions during the breeding season, and demonstrates the role of model-based research in linking foraging behaviour with reproductive success to anticipate seabirds' demographic and spatial responses to climate-mediated environmental and trophic changes in the North Atlantic Ocean

Keywords: *foraging behaviour; population ecology; climate change; system-dynamics; agent-based models; Cory's shearwater; Cape Verde shearwater.*

Resumo

O aquecimento global tem vindo a forçar mudanças persistentes e sem precedentes no ambiente marinho, impondo um grande desafio aos cientistas, decisores políticos e gestores ambientais na busca de soluções para a sustentabilidade futura dos oceanos. Os principais predadores marinhos, como as aves marinhas, são amplamente regulados por dinâmicas tróficas, oferecendo uma visão particular sobre o estado dos ecossistemas marinhos e suas mudanças ao longo do tempo. Por conseguinte, prever as respostas das aves marinhas a variações na disponibilidade de recursos e antecipar a sua capacidade para lidar com condições ambientais futuras pode fornecer informações relevantes para a gestão e conservação de espécies e habitats marinhos. Nesta tese usei conjuntos de dados de rastreamento por GPS de cagarras-do-atlântico e cagarras-de-cabo-verde (*Calonectris borealis* e *Calonectris edwardsii*, respetivamente) e abordagens de modelação mecanicista, como dinâmica de sistema e modelos baseados em agentes, para explorar hipóteses relacionadas com a ecologia de procura de alimento por cagarras reprodutoras no Oceano Atlântico Norte (arquipélagos das Berlengas, Açores, Madeira e Cabo Verde). Em particular, investiguei os mecanismos de nível individual subjacentes ao comportamento de procura de alimento das cagarras durante a época de cria e avaliei estratégias comportamentais que permitem aos indivíduos maximizar a sua aptidão em condições de disponibilidade alimentar contrastantes. Um ênfase especial foi dado aos processos relacionados com as capacidades sensoriais e cognitivas utilizadas pelas aves para localizar presas no mar, bem como a necessidade de equilibrar o esforço de procura de recursos alimentares para consumo próprio e para a alimentação das crias dentro das restrições impostas pela fase do ciclo reprodutor em que as aves têm de efetuar deslocações regulares e periódicas ao ninho. Também avaliei desequilíbrios ecológicos desencadeados por mudanças ambientais induzidas pelo Homem, com consequências para a ecologia reprodutiva das cagarras por meio de pressões predatórias nos locais de reprodução. Este estudo revelou: 1) uma ligação potencial entre o comportamento de procura de alimento das cagarras e os processos de decisão associados ao momento de chegada ao ninho; 2) um efeito sinérgico entre a procura olfativa e com base em informações sociais para a procura ótima de alimento pelas aves marinhas pelágicas; 3) estratégias flexíveis de comportamento parental e cooperação para a alimentação das crias e decisões de procura de alimento; e 4) diretrizes para programas locais de gestão com implicações para a conservação das cagarras. Esta tese termina com a integração dos resultados numa proposta de modelação que visa utilizar informação acerca do comportamento e da ecologia de procura de alimento por aves marinhas na conservação dos ecossistemas marinhos, incluindo avanços conceptuais e técnicos para a sua futura implementação usando a cagarra-do-atlântico como espécie alvo. No geral, este estudo avança compreensão acerca da flexibilidade comportamental das cagarras a variações nas condições de disponibilidade de alimento durante a época de reprodução e demonstra o papel da investigação baseada em modelos na ligação do comportamento de procura de alimento com o sucesso reprodutivo para antecipar respostas demográficas e espaciais das aves marinhas às mudanças ambientais e tróficas induzidas pelo clima no Oceano Atlântico Norte.

Palavras chave: *comportamento de procura de alimento; ecologia populacional; alteração climática; dinâmicas de sistema; modelos baseados no agente; cagarra-do-atlântico; cagarra-de-cabo-verde.*

List of Abbreviations

ABM - Agent-based model

ARS – Area restricted search

CHL - Chlorophyll-a concentration

CI – Confidence interval

EmbC - Expectation-Maximization binary Clustering

ES – Energy score

FAD – Foraging-allocation decision

FKD - Fixed kernel density

GPS – Global positioning system

LE - Local enhancement

OS - Olfactory search

OSLE - Olfactory search with local enhancement

SST – Sea surface temperature

US - Uninformed search

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General Introduction

Impacts of climate change in marine ecosystems

Pressures on the marine environment have increased dramatically at the global level, leading to rapid and diverse changes in the structure and functioning of marine systems (Halpern et al. 2008; Hoegh-Guldberg and Bruno 2010). Direct anthropogenic perturbation in marine ecosystems is driven by the intensive use of agricultural fertilizers, overexploitation of fish stocks, spreading of invasive species and other sources of coastal and oceanic habitats degradation, such as the increasing of aquaculture production and offshore wind-farms installation (Korpinen et al. 2021). Additionally, rising levels of atmospheric carbon dioxide (i.e. human-made interference with climate) have also been causing widespread, long-lasting physical and chemical changes in the marine environment (Doney et al. 2012; Howes et al. 2015). The primary direct consequences are increasing ocean temperatures and acidity, with ocean warming creating a host of additional changes such as rising sea level, increased ocean stratification, decreased sea-ice extent, and altered patterns of ocean circulation, precipitation, and freshwater input (IPCC 2019). At the biological level, changes in seawater temperature and chemistry interfere with the physiology, behaviour, and demographic traits of organisms, driving shifts in the size, structure and distribution of populations (Somero 2012). These, in turn, lead to altered species interactions and food web dynamics, thereby affecting the structure and diversity of communities and, ultimately, the functioning of ecosystems (McCauley et al. 2015).

The marine pelagic environment (i.e. both coastal waters and open ocean) is a major focus of concern regarding the potential impacts of anthropogenic climate change given its socio-economic importance for fisheries (Pauly et al. 2002), and environmental relevance for the regulation of climate itself (Hays et al. 2005). Among the most recognised effects of climate change in the structure and functioning of pelagic ecosystems are changes in large-scale and regional oceanographic processes (i.e. oceanic circulation, stratification and upwelling regimes), with negative consequences in nutrient availability and bottom-up control on food chains (Brierley and Kingsford 2009). For example, the stratification of the upper ocean plays a fundamental role in regulating the interplay between light availability for photosynthesis and nutrient supply from the deep to upper layers of the ocean (Sigman and Hain 2012). However, the warming of the ocean surface is leading to increased vertical stratification and water column stability, reducing nutrient availability to the euphotic zone and thus reducing the productivity of both primary and secondary producers (Doney 2006; Howes et al. 2015). This cause changes in the abundance and distribution of low- and mid-trophic level consumers (e.g. squid, anchovies, and sardines), which affect higher trophic level species (i.e. larger fishes, seabirds and marine mammals) (e.g. Serpetti et al. 2017; Campana et al. 2020). Therefore, anthropogenic climate change has pronounced implications for the productivity of pelagic ecosystems via warming-induced alterations in physical forcing, affecting all levels of ocean biological organization and function.

The North Atlantic Ocean includes a tremendously large and diverse environment, which has been experiencing rapid modifications as a result of global climate change. In the last decades, the North Atlantic Ocean has warmed significantly (Palmer and Haines 2009), causing, among others, biogeographic shifts in species ranges, changes in ocean circulation patterns and marine productivity, and intensification of extreme weather events. For example, over the past fifty years, increasing ocean temperatures have been related to a north-ward shift in the distribution of many plankton and fish species inhabiting this area (e.g. Beaugrand et al. 2002; Adams et al. 2018). Causal relationships between sea surface temperature and hurricane occurrence and activity were also demonstrated, which have altered the frequency of disturbance regimes, leading to changes in coastal ecosystems structure and functioning (Saunders and Lea 2005). Studies also suggest that climate-driven changes in ocean circulation patterns have been responsible for declining nutrient concentrations and marine productivity in the North Atlantic Ocean (Johnson et al. 2013; Spooner et al. 2020). Nevertheless, the warming of the ocean is not spatially or temporally uniform owing to variable ocean currents, wind patterns, and interaction with natural modes of climate variability, such as those related with the North Atlantic Oscillation (Lozier et al. 2008; 2011). Therefore, climate impacts on marine communities might vary in space and time according to the heterogeneous distribution of these environmental stressors, probably emerging at species- and/or site-specific levels (Stenseth et al. 2002).

Seabirds as ecological indicators of marine environmental changes

Marine pelagic ecosystems are extremely complex environments, thus difficult to evaluate in their totality. This poses the need of an integrative view of the effects of climate change and anthropogenic pressures in the pelagic environment, namely by using indicator species capable of summarizing large quantities of information into a set of relevant and accessible signals (Durant et al. 2009). When compared to other groups of marine species, seabirds offer particular advantages for this assessment (Furness and Camphuysen 1997), namely because: 1) they are conspicuous animals in an environment in which most other species live under water; 2) they cover vast areas of the pelagic realm, feeding at a wide range of trophic levels and in a broad spectrum of marine habitats, thereby representing optimal sampling tools of fish stocks across different spatio-temporal scales; 3) most species are colonial and congregate annually at specific locations to reproduce thus allowing measurements of a wide variety of demographic, behavioural and physiological parameters. Furthermore, being placed at or near the apex of most marine food chains, seabirds are largely controlled by bottom-up (e.g. changes in primary productivity) and top-down (e.g. overfishing) processes, thereby offering unique insights into ecosystem status and change (Piatt et al. 2007).

Since lower trophic-level prey (i.e. zooplankton, squid, and fish) fluctuate in response to changing ocean conditions (e.g. ocean temperature and physical forcing), the main indirect influence of climate on marine predators is through the regulation of food availability (Sydeman et al. 2015a). In particular, changes in prey abundance, species composition, energetic quality or synchronisation may have profound effects on seabirds. For example, population declines and poor breeding success for seabirds worldwide are often connected with a strong depletion of the most common and abundant prey types (e.g. Frederiksen et al. 2004, Kowalczyk et al. 2014, Grémillet et al. 2016). In other cases, temporal mismatches between prey recruitment and seabird requirements (due to changes in the timing of productivity during spawning of prey species) have been attributable to changes in the reproductive success and survival (e.g. Cohen et al. 2014; Regular et al. 2014). At the physiological and behavioural levels, shifts in prey availability have been related to seabirds food-related stress levels (e.g. Kitaysky et al. 2007; 2010) and changes in foraging and offspring provisioning behaviour (e.g. Suryan et al. 2000; Divoky et al. 2015; Lamb et al. 2017). Intra and inter decadal climate variability (i.e. oceanographic conditions associated with large-scale climatic anomalies), especially in upwelling systems, also shows strong linkages between climate forcing and seabird distributions, phenology and demography, with food availability assumed to be the key driving mechanism (e.g. Durant et al. 2004; Sydeman et al. 2006, 2015b; Wolf et al. 2009; Bost et al. 2015; Carroll et al. 2016). Therefore, seabirds physiological, behavioural, and demographic responses to environmental variability can reflect changes in physical oceanic attributes and food web dynamics via bottom up effects, thereby serving as an early warning system of climate-mediated chances in marine ecosystems.

Ecological modelling in the context of climate change

Although the number and complexity of modelling techniques used to explain and predict species distributions and abundances have increased substantially over the past decades (e.g. Species Distribution Models, Robinson et al. 2017; Matrix Population Models, Fujiwara and Diaz-Lopez et al. 2017), a major challenge remains when the goal is to integrate the ecological processes that shape species occurrence patterns and their population dynamics (e.g. physiologically and behaviourally based environmental constraints that influence their distribution and abundance; Evans et al. 2015; Johnston et al. 2019). In fact, modelling efforts have largely focused on correlative analyses of observed species-environment associations (Melo-Merino et al. 2020). However, since these approaches correlate environmental and climatic variables directly to species occurrence or abundance, they are usually limited in their biological realism and in their transferability to novel environments (Dormann et al. 2012; Yates et al. 2018). On the other hand, mechanistic modelling approaches, such as System Dynamics and Agent-Based Models (ABMs), have been developed to reproduce the structure and functioning of real-life systems in a more realistic and dynamic way (Jørgensen 2001; DeAngelis and Mooij 2005; Grimm and Berger 2016). In particular, these models account for process-based changes in the state of a system, thus providing a mechanistic understanding of the species responses to modified environmental conditions (e.g. Carter et al. 1999; Faust et al. 2003; Zurell et al. 2015; Bastos et al. 2016a,b; Arosa et al. 2017; Johnston et al. 2018; Boyd et al. 2018). The main difference between System Dynamics and ABMs is that, while System Dynamics seek to explain the dynamic behaviour of complex systems through aggregated system-level properties (e.g. age, breeding status or population structure), ABMs are particularly suitable when the goal is to explicitly represent individual animals and their behavioural decisions. Therefore, ABMs can be especially useful whenever variability amongst individuals, local interactions with the environment, or adaptive behaviour are considered essential (van der Vaart et al. 2016).

Integrating the behavioural mechanisms that underlie seabird population responses to environmental variability is fundamental to formulate increasingly robust and accurate predictive models in the context of climate changes (Palacios et al. 2013). In fact, behavioural strategies (e.g. those that arise from social, foraging or reproductive activities) influence how animals respond to environmental perturbation (Wong et al. 2015), which can directly or indirectly affect their fitness and spatial ranges (e.g. Thorne et al. 2015; Jeanniard-du-Dot et al. 2017); the very key parameters determining populations dynamics and occurrence patterns. Thus, identifying factors that influence seabird behaviour (e.g. resources availability and distribution but also cognitive abilities, social learning, parent-offspring conflict, pair cooperative behaviour) may provide important information to predict species responses to future environmental conditions. In this regard, ABMs have been created to develop a mechanistic understanding of marine top predators behaviour (e.g. Liukkonen et al. 2018; Chudzinska et al. 2021), including of individual's responses to environmental constraints (e.g. Wiedenmann et al. 2011; Langton et al. 2014; Boyd et al. 2016a,b; Dodson et al. 2020; Hentati-Sundberg et al. 2021). Built on a bottom-up approach, the integration of individual-level mechanisms can therefore provide a comprehensive understanding of the potential environmental effects on seabird behaviour that might influence their distribution and population trends in the future (e.g. Massardier-Galatà et al. 2017). However, predicting marine populations responses to projected climate change using individual-level frameworks remains relatively poorly explored, with few attempts being mostly directed to fish species (e.g. Triantafyllou et al. 2019; Boyd et al. 2020); despite the need for reliable predictions of top predators responses, especially in light of current management frameworks like ecosystem-based management or marine spatial planning (e.g. Sainsbury et al. 2000; Levin et al. 2009, Foley et al. 2010; Frazão Santos et al. 2020).

Predicting shearwaters responses in the North Atlantic Ocean

Understanding how climate change is transforming marine ecosystems is fundamental to find effective solutions for the future sustainability of the world's oceans. In this sense, Cory's and Cape Verde shearwaters (*Calonectris borealis* and *Calonectris edwardsii*, respectively) represent promising indicator species to evaluate the impacts of climate-induced ecosystem changes in the North Atlantic Ocean because: (1) they are long-lived marine top predators that breed in the North Atlantic, (2) are medium-sized species, enabling to carry Global Positioning System (GPS) devices and thus obtain relevant behavioural information, (3) are relatively abundant and well-studied species, (4) breed colonially in places where there is fairly good access to nesting sites, and (5) are sensitive to environmental and climatic variability. In fact, long-lived predator species are the most endangered and sensitive group of animals to environmental perturbation due to their extreme life history traits (e.g. high survival, low fecundity and an usually considerable degree of specialization; Warham 1990), which make them particularly vulnerable to changing conditions during the breeding season, i.e. deteriorating environmental conditions (e.g. poor resource availability) will be firstly reflected in terms of reproduction rather than adult survival (Stearns 1992). Therefore, the ability to identify, quantify and predict modifications in shearwaters breeding responses can provide relevant information about the distribution and extent of priority marine habitats and hotspots of change in the North Atlantic Ocean. Furthermore, being species that present conservation interest at local and global levels, evaluating and predicting their population responses to changes in the North Atlantic is also important in the field of marine biological conservation.

Cory’s and Cape Verde Shearwaters: Life-history traits, conservation status and foraging behaviour

Cory’s and Cape Verde shearwaters are medium-sized long-winged seabird species, belonging to the family Procellariidae, included in the bird order Procellariiformes (or tubenoses; also including petrels and albatrosses). They are wide-ranging oceanic birds, spending the majority of their life in the open sea (where they mainly feed on small fishes, crustaceous and squid; Granadeiro et al. 1998a), coming ashore to islands and open cliffs only to breed. During reproduction, they behave as central place foragers, thus having their distribution limited to a central area around breeding colonies (Cairns 1988). As long-lived animals (with life spans reaching up to 25 years in the case of Cory’s shearwaters; Fransson et al. 2017), the individuals present extreme life history strategies (Warham 1990), i.e. they exhibit strong philopatry and late sexual maturity; are monogamous, developing long-term pair bonds that may last for an entire life; nest in cavities and burrows where they lay one single egg with no clutch replacement, thus presenting low reproductive rates. The incubation period lasts for approximately two months and is shared between males and females, and both parents feed the chick for about another two months (Granadeiro 1991). After breeding in the North Atlantic, the vast majority of Cory’s and Cape Verde shearwaters migrate towards the south hemisphere, thus being considered trans-equatorial migrators. Cory’s shearwaters commonly select wintering-areas in the coast of Brazil, Namibia, South Africa and Mozambique (BirdLife International 2021a), although new evidences suggest that some individuals choose the waters off the Canadian coast also as non-breeding grounds (Gjerdrum et al. 2018). Cape Verde shearwaters spend the non-breeding period in the coast of Brazil (BirdLife International 2021b).

The Cory’s Shearwater (*Calonectris borealis*, Cory 1881) is one of the most abundant pelagic seabird species breeding in Portuguese islands (i.e. Berlengas, Azores and Madeira archipelagos), which globally comprise 85% of the world breeding population (BirdLife International 2021a). Due to its extremely large range and population size (250 000 breeding pairs), the species conservation status is considered of ‘Least Concern’, although the population trend is currently unknown (BirdLife International 2021a). Despite common and widespread in Azores and Madeira, birds breeding in the Berlengas archipelago (off the Portuguese mainland) present ‘Vulnerable’ conservation status, given its small population size (less than 1000 mature individuals; see also Lecoq et al. 2011) and very restricted area of occupancy (less than 150 ha) (Cabral et al. 2005). The primary threats to this species include interaction with fisheries (i.e. incidental bycatch by longline fisheries) (Granadeiro et al. 2006; Ramos et al. 2012), and nest predation by invasive, non-native species (i.e. rats and feral cats) (Hervías et al. 2013). Local pressures at breeding grounds can also include predation by native species, such is the case of one colony from Madeira where chicks are predated by Madeiran wall lizards (*Teira dugessii*) (Matias et al. 2009), and in the Berlengas where yellow-legged gulls (*Larus michaelis*) exert predatory pressure on Cory’s shearwaters’ eggs (Lecoq et al. 2010, 2011).

The Cape Verde shearwater (*Calonectris edwardsii*, Oustalet 1883) is an endemic species from the Cape Verde archipelago. This species is listed as ‘Near Threatened’ owing to its moderately small population (10 000 breeding pairs) and range size, although more information may warrant its up-listing to a higher threat category (BirdLife International 2021b). Uncontrolled levels of harvest at breeding grounds are supposed to be one of the main threats to this species, but more information is still needed to uncover the effect of other potential threats, such as the interaction with fisheries and predatory pressure (BirdLife International 2021b).

Due to differences in geographic location, the Berlengas, Azores and Madeira archipelagos represent particular and distinct foraging conditions for breeding Cory’s shearwaters (Paiva et al. 2010a). In Azores and Madeira, birds breed within an oceanic environment usually characterized by low marine productivity in neighbouring pelagic waters. These conditions induce individuals to search for feeding areas with enhanced marine productivity approximately 500 km north of Azores, over seamounts and frontal regions, and around 650 km east of Madeira, towards the large neritic system of the African continental shelf (Paiva et al. 2010b). Under such circumstances, breeding birds commonly adopt a bimodal foraging strategy, intercalating short foraging trips around breeding sites used mainly to feed their chicks, with long travels towards regions of higher resource profitability for the maintenance of their own body condition (Magalhães et al. 2008; Paiva et al.

2010a,b). On the other hand, in Berlengas, the dominant neritic environment is characterized by high productive coastal upwelling events along the Portuguese continental platform, providing profitable foraging areas in the colony surroundings (Paiva et al. 2010a). In this neritic colony, Cory's shearwaters tend to describe a unimodal foraging pattern, mostly performing short foraging trips that presumably allow to supress both chicks and adults' energetic requirements (Paiva et al. 2010b). Cory's shearwaters also reveal behavioural flexibility in shifting foraging patterns between years within the same colony, which has been associated with changes in the individuals' foraging range, feeding habits, body condition, chick growth and breeding success (e.g. Granadeiro et al. 1998b; Paiva et al. 2013; 2017; Ceia et al. 2014). Related to this, Paiva et al. (2013) showed a negative effect of climatic stochasticity (depicted by negative NAO index values) in ocean productivity regimes at Berlengas, which triggered an abrupt decrease in the abundance and availability of prey and, consequently, a decrease in the breeding success of Cory's Shearwaters. A recent study also shows that Cory's shearwaters breeding in neritic (Berlengas) and oceanic (Azores) areas modify foraging behaviour and individual fitness in response to large-scale climatic anomalies in the North Atlantic Ocean, with variations in food availability caused by shifts in regional oceanographic processes assumed as the key mechanism (Pereira et al. 2020).

In the tropics, Cape Verde shearwaters commonly alternate short foraging trips in the less productive foraging areas surrounding breeding colonies, and long foraging trips towards areas of great productivity in the West African coast, 600 km east of Cape Verde (Paiva et al. 2015). Previous studies also suggest that inter-annual variations in oceanographic conditions affect the foraging behaviour and trophic ecology of Cape Verde shearwaters (Paiva et al. 2015; Cerveira et al. 2020), with consequences for chick growth (Ramos et al. 2018).

Thesis structure and overall aims

The main goal of this thesis is to advance understanding of shearwaters flexible responses to variations in foraging conditions during the reproductive season, and demonstrate the applicability of model-based research in linking foraging behaviour with breeding performance to anticipate seabirds demographic and spatial responses to environmental and trophic changes. The thesis is structured in four chapters, in which I took advantages of GPS tracking datasets and advances in ecological modelling to explore questions related to the foraging ecology and conservation of shearwaters breeding in the North Atlantic Ocean. The specific objectives of this study are: 1) investigate individual-level mechanisms underlying shearwaters foraging behaviour during chick rearing; 2) evaluate flexible behavioural strategies that enable individuals to maximize their fitness under contrasting foraging conditions; 3) explore the links between individual behaviour, population-level processes and threats for the conservation of marine species and their habitats.

Chapter 1. Nocturnal foraging as a driving mechanism of the shearwaters' nest attendance patterns throughout the lunar cycle

In the first chapter, nest attendance patterns of breeding shearwaters were investigated in relation to oceanographic and nocturnal light conditions during mid-chick rearing, using a long-term GPS tracking dataset (2007-2017) from Cory’s and Cape Verde shearwaters in the Berlengas, Azores, Madeira and Cape Verde archipelagos. Inter-annual changes in oceanographic conditions around each colony were evaluated using proxies for marine productivity (Chlorophyll-a concentration and sea surface temperature anomaly) and metrics of shearwaters foraging effort (foraging trips distance and duration). This study improves understanding about the mechanisms shaping at-night nest attendance behaviour by shearwaters during chick rearing, highlighting the role of long-term empirical studies to investigate the individuals responses to changes in foraging conditions around breeding sites.

Bastos R, Martins B, Ramos JA, Paiva V, Pereira J, Ceia F, Gouveia C, Rodrigues C, Santos M, Cabral JA (*under review*). Nocturnal foraging as a driving mechanism of the shearwaters’ nest attendance patterns throughout the lunar cycle. Journal of Experimental Research in Marine Biology and Ecology.

Chapter 2. Oceans of stimuli: an individual-based model to assess the role of olfactory cues and local enhancement in seabirds' foraging behaviour

In the second chapter, an individual-based model was developed to investigate sensorial abilities (olfactory senses) and cognitive processes (social information transfer through local enhancement) underlying Cory's shearwaters foraging behaviour. The model was parameterized with GPS movement data from Cory's shearwaters tracked during 1-day foraging trips around the Corvo island (Azores archipelago), and the foraging efficiency of virtual individuals was analysed considering hypothetical scenarios of local foraging conditions and densities of foraging individuals. The environmental scenarios considered simulate a gradient of environmental conditions based on proxies for marine productivity (Chlorophyll-a concentration, sea surface temperature and bathymetry) that, in the absence of prey data, were assumed to recreate realistic scenarios of resources availability around the Corvo Island. This study provides a mechanistic understanding of shearwaters space use patterns during local foraging trips, highlighting the role of spatially-explicit ABMs to investigate searching strategies for the optimal foraging of pelagic seabirds.

Bastos R, Martins B, Cabral, JA, Ceia F, Ramos J, Paiva V, Luís A, Santos M (2020). Oceans of stimuli: An individual-based model to assess the role of olfactory cues and local enhancement in seabirds' foraging behaviour. Animal Cognition, 23(4): 629-642.

Chapter 3 - Mechanisms of parental behaviour and cooperation in chick provisioning decisions by a long-lived seabird: insights from a dynamic model with Cory's shearwaters

In the third chapter, an energy-budget model was constructed to explore the chick provisioning dynamics of Cory's shearwaters during chick rearing (from egg hatching to fledging of the young), considering physiologic constraints and behavioural decisions of breeding pairs. The model was parameterized with empirical data from Cory's shearwaters breeding at Selvagem Grande (Madeira archipelago). Potential mechanisms underlying foraging allocation-decisions of breeding parents were investigated by assuming adaptive compromises among the three family members (the focal bird, the chick and the partner). To test whether the optimal solutions to these compromises change along a gradient of resources availability, variations in local foraging conditions were recreated through changes in the adults' mass gains during short foraging trips. This study improves understanding about the mechanisms driving shearwaters foraging decisions throughout chick rearing , highlighting the role of energy-budget models to link foraging behaviour with breeding performance of central place foragers.

Bastos R, Santos D, Ramos J, Paiva V, Ceia FR, Ceia RS, Luís A, Santos M, Cabral JA (*submitted*). Mechanisms of parental behaviour and cooperation in chick provisioning decisions by a long-lived seabird: insights from a dynamic model with Cory's shearwaters. Marine Ecology Progress Series.

Chapter 4 - Localized control of opportunistic, overabundant species in protected areas: a retrospective modelling approach encompassing future scenarios

In the fourth chapter, a population model was created to disentangle the effects of environmental changes (availability of anthropogenic food resources) and conservation management actions (culling and fertility control) in the long-term population trends (1978-2040) of a recognized potential threat to the reproductive ecology of Cory's shearwaters at Berlenga Island: the yellow-legged gull (*Larus michahellis*). The model integrates demographic data spanning the periods before and after the closure of open-air dumps in Portugal, and the effects of culling and egg destruction campaigns carried out to control this opportunistic species at the Berlenga Natural Reserve. Simulation results allowed to evaluate the extent to which past control measures contributed to the decrease of yellow-legged gulls on the Berlenga, and to predict the outcome of future management in the current context of seagulls' restricted access to anthropogenic resources. This study highlights the role of population modelling approaches in providing guidelines and compromises for the management and conservation of marine species and their habitats.

Pinto Eva, **Bastos R (as corresponding author),** Luís A, Cabral JA (2021). Localized control of opportunistic, overabundant species in protected areas: a retrospective modelling approach encompassing future scenarios. Animal Conservation. https://doi.org/10.1111/acv.12682

In the final section, I summarise the key findings of the thesis and discuss their implications for the study of shearwaters' behavioural ecology and for the control of threats in their breeding sites. This section ends with recommendations for future research, namely the presentation of a modelling framework that aims to use information about seabirds foraging behaviour and ecology into the conservation of marine ecosystems, including conceptual and technical advances for its future implementation using the Cory's shearwater as a target model species.

Bastos R, Garaboa A, Paiva V, Ramos JA, Pereira J, Santos M, Alvarez I, Muñuzuri V, Cabral JA (*in preparation*). The role of pelagic seascape structure and composition on seabirds habitat selection: The study-case of Cory’s shearwaters in the North Atlantic Ocean.

Chapter 1

Nocturnal foraging as a driving mechanism of the shearwaters' nest attendance patterns throughout the lunar cycle

Photograph by Beatriz Martins 2018

1.1 Abstract

The moon cycle has long been recognized as a driving factor of animals' behavioural patterns. However, its influence on seabirds' nocturnal behaviour remains poorly understood. Using a long-term GPS tracking dataset (2007-2017) from Cory's and Cape Verde shearwaters in the Berlengas, Azores, Madeira and Cape Verde archipelagos, North Atlantic Ocean, we investigated nest attendance patterns of breeding birds in relation to oceanographic and nocturnal light conditions during mid-chick rearing. We intended to understand if inter-annual changes in oceanographic conditions around each colony were related with timing of nest arrival and respective light intensity at burrow entrance. For this, oceanographic conditions were evaluated using proxies for marine productivity and metrics of shearwaters' foraging effort. We also wanted to investigate if birds adjusted nest attendance in relation to moonlight throughout the lunar cycle, and whether these patterns changed with contrasting oceanographic conditions. Shearwaters stayed longer at sea after sunset in years of good oceanographic conditions, while returned ashore earlier in years of poor conditions, under twilight. In addition, breeding birds seemed little influenced by moonlight at colonies, although this did not seem to be the case at sea. In particular, breeding shearwaters adjusted nest arrivals with the onset of waning moon nights (nights starting without moon), but delayed nest entrances throughout waxing moon nights (nights entailing a growing period of moonlight until moonset). However, this pattern was not extensible to years of poor foraging conditions when birds returned ashore early regardless of moonlight conditions. Combined, these results show that the nest attendance behaviour is mediated by moonlight in Cory's and Cape Verde shearwaters, a pattern that seems to be regulated by prevailing oceanographic and foraging conditions.

Keywords: *Calonectris borealis*; *Calonectris edwardsii*; foraging conditions; GPS-tracking; moonlight.

1.2 Introduction

The influence of moon cycles has long been recognized as a driving factor of physiological and behavioural patterns across a wide range of animal groups, from synchronization of mass spawning events in corals (Harrison et al. 1984) and amphibians (Grant et al. 2013) to changes in communication patterns of birds (Penteriani et al. 2010) or in the nocturnal activity of primates (Fernández-Duque et al. 2010). Among burrow-nesting procellariid species (petrels and shearwaters) the vast majority are strictly nocturnal on their breeding colonies, returning ashore mostly after dusk and departing for the sea before sunrise (Warham 1990). Some species are also known to decrease colony attendance in the brightest nights of the lunar cycle, reducing aerial and vocal activity under intense moonlight at colony grounds (Storey and Grimmer 1986; Bretagnolle 1990). This behaviour has been commonly interpreted as an anti-predator strategy (i.e. 'predation avoidance' hypothesis) to reduce predation or agonistic interactions with diurnal predators (Harris 1974; Watanuki 1986; Telfer et al. 1987; Bretagnolle 1990; Mougeot and Bretagnolle 2000; Keitt et al. 2004; Rubolini et al. 2015). However, the "predation avoidance" theory becomes difficult to interpret when birds breed in the apparent absence of predators or suffer low predatory pressures (i.e. large-bodied species with strong defence mechanisms) (e.g. Bretagnolle 1990; McNeil et al. 1993; Bourgeois et al. 2008; Van Tatenhove et al. 2018).

From another perspective, the absence of birds on land during intense moonlight has also been proposed as a consequence of foraging efficiency ('foraging efficiency' hypothesis) (Imber 1975). The 'foraging efficiency' theory proposes that the cause of this phenomenon is related to contrasting at-sea foraging opportunities, induced by an increase in prey availability during dark nights (i.e. vertical migration of squid, fish and crustaceans) (Boden and Kampa 1967; Hernández-Leon 2001). Thus, lower accessibility of food resources on moonlit nights means that birds need to increase foraging effort (i.e. spend more time at sea during the night), which ultimately lead to a relative decrease in nest attendance on brighter nights (Imber 1975; Klomp and Furness 1992; Mougeot and Bretagnolle 2000). Another important aspect in this regard is that, if nest attendances are influenced by prey accessibility throughout the lunar cycle, this behaviour should also reflect variations in the availability of resources at broader spatio-temporal scales (Cairns 1987). Therefore, investigate the individuals' nest attendance responses to inter-annual fluctuations in local foraging conditions is important to understand the mechanisms underlying nest attendance behaviour by seabirds.

The Cory's and Cape Verde shearwaters are medium to large size seabirds that are predominantly nocturnal on breeding sites. At colonies, Cory's shearwaters are generally more active in the beginning of the nights (i.e. 1-2 hours after arrival) and before leaving for the sea at dawn (Granadeiro et al. 1998c). The period they remain on land can be highly variable (between 1 and 4 hours; Granadeiro et al. 1998c), during which they stay inside the burrow or in the outside, close to the nest (Pers. obs). To date, nest attendance patterns of Cape Verde shearwaters remain unknown. Interestingly, one of the first studies that empirically supported the foraging theory involved Cory's shearwaters, which tended to return ashore less frequently on full moon nights, feeding their chicks later and with smaller meal sizes when compared to new moon nights (Klomp and Furness 1992). However, further studies did not clearly confirm the influence of lunar cycles on Cory's shearwaters' colony attendance patterns (Mougin et al. 2000; Granadeiro et al. 2009) nor at-night activity rhythms and time of nest arrival (Granadeiro et al. 1998c).

Using a long-term dataset of GPS tracked individuals from the Azores, Berlengas, Madeira and Cape Verde archipelagos, we investigated the nest attendance patterns of breeding shearwaters during the mid-chick rearing period. In particular, we were interested in understanding how oceanographic and nocturnal light conditions shape the return of birds to the nest. For this, we firstly described inter-annual patterns of oceanographic conditions around each colony and addressed how such conditions were related with changing patterns of nest attendance by breeding birds, in terms of timing of burrow entrance and respective light intensities at arrival. Inter-annual variations in oceanographic conditions around each colony were evaluated through proxies for marine productivity (i.e. chlorophyll-a concentration and sea surface temperature anomaly) and metrics of shearwaters' foraging effort (i.e. duration of foraging trips). We also intended to understand if birds adjusted nest attendance in relation to moonlight conditions throughout the lunar cycle, and whether these patterns changed with contrasting oceanographic conditions. According to the foraging efficiency theory, we expect a positive correlation between timing of nest arrivals and moonlight intensity throughout the lunar cycle. Furthermore, if nest attendance behaviour is a flexible trait that diverges in relation to prevailing foraging conditions, we also expect to find changes in timing of nest arrival somehow associated with differences in oceanographic conditions around breeding sites.

Overall, this study will provide new insights on shearwaters' nest attendance behaviour in relation to oceanographic and nocturnal light conditions, allowing a better understanding of the processes and mechanisms behind the observed patterns. Also, if shearwaters adjust nest attendance to fluctuations in resources availability, this behaviour can be used as a proxy for prey abundance around breeding sites, offering important insights on the marine ecological status and potential changes at local scales.

1.3 Methods

1.3.1 GPS tracking datasets

To investigate the nest attendance and nocturnal activity patterns of breeding Cory's and Cape Verde shearwaters, a long-term dataset of tracked individuals from the Corvo

Island (Azores), Berlenga Island (Berlengas), Porto Santo Island (Madeira) and Raso Islet (Cape Verde) was used (Figure 1; Appendix A).

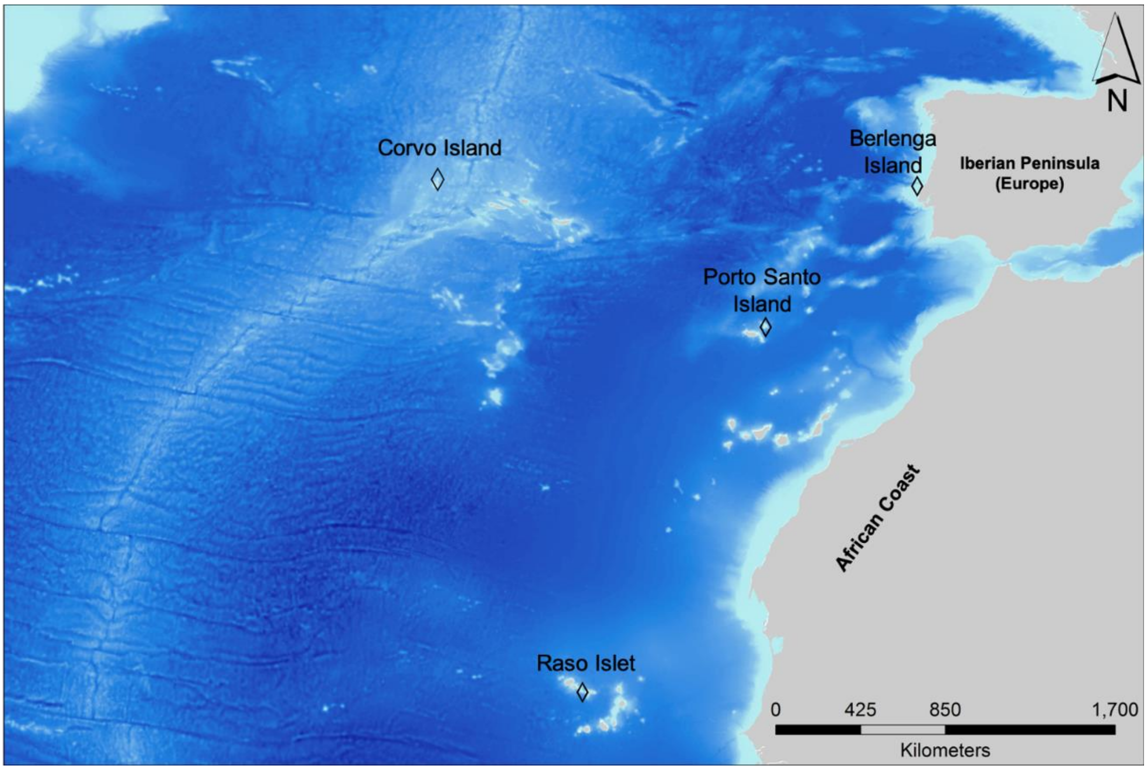


Figure 1 - Location of the study colonies of Cory's shearwaters (*Calonectris borealis*) in the Corvo Island (Azores archipelago), Berlenga Island (Berlengas archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

The phenological period monitored corresponds to the mid chick rearing stage in all study colonies, ranging between 26 of July and 13 of September in Corvo; 10 of August and 20 of September in Berlenga; 29 of July and 23 of August in Porto Santo; and 24 of August and 3 of October in Raso Islet (Appendix A). A total of 374 foraging trips from 65 tracked birds was gathered during 4 years in Corvo, 790 foraging trips from 132 tracked birds during 9 years in Berlenga, 116 foraging trips from 24 tracked birds during 4 years in Porto Santo, and 319 foraging trips from 43 tracked birds during 4 years in Raso (Appendix A). Overall, the number of sampled waning moon nights and waxing moon nights was respectively 20 and 34 for Corvo, 45 and 64 for Berlenga, 23 and 18 for Porto Santo, and 17 and 41 for Raso (Appendix A). Time of burrow entrance after a foraging trip was calculated using accurate positioning data obtained from GPS loggers, defined as the nearest GPS position from the nest, calculated with an accuracy of 5 or 10 minutes (Appendix A). Details about the data loggers and their deployment are given by Paiva et al. (2010a; 2015).

1.3.2 Patterns of nest arrival in relation annual variation in oceanographic conditions

1.3.2.1 Analysis of timing of nest arrival and light intensity at burrow entrance

To investigate potential variations in the shearwaters' inter-annual patterns of nest attendance, a Kruskal-Wallis was used to test whether timing of nest arrival and light intensity at burrow entrance diverged among monitoring years per colony. Timing of nest arrival was expressed as the time elapsed (in minutes) between sunset and the arrival at the nest. The time of sunset was extracted for each day and study site location from http://aa.usno.navy.mil/data/docs/RS_OneYear.php, considering the period of the day when the upper edge of the sun was tangent to the horizon. Levels of light intensity at nest arrival were estimated using a compilation of astronomic models to assess spatial and temporal explicit measures of light intensity at the earth's surface (Regular et al. 2011). Light intensity was expressed in Wm^{-2}, assuming the solar, lunar and star irradiance, taking into account the date and the Greenwich mean time of nest arrivals, and the geographic position of each colony. Because estimates of twilight intensity levels were not available due to the lack of available astronomic models (Regular et al. 2011), total irradiance was modelled as a function of solar elevation during twilight (Spitschan et al. 2016). Therefore, light intensity for shearwaters' nest arrivals at dusk and dawn were predicted by assuming a sigmoidal relationship between the total irradiance at twilight (spanning from 1 Wm^{-2} to 0.001 Wm^{-2}, Regular et al. 2011) and the corresponding period (in minutes) of twilight for each colony as a proxy for solar elevation (extracted from https://www.timeanddate.com/sun/). Total irradiance from the sun and moon was calculated after correcting for extinction of absolute irradiance from the earth's atmosphere (Regular et al. 2011). The Kruskal-Wallis Test was performed using the ´kruskal.test´ function in the R package ´stats´ (R Development Core Team 2020), and all pairwise *pos-hoc* multiple comparisons were analysed using a Dunn's test (for groups with unequal numbers of observations), applying the ´DunnTest´ function in the R package ´DescTools´ (Signorell et al. 2016; R Development Core Team 2020). Light intensity profiles of nest arrivals were plotted for each colony, given the annual proportion of burrow entrances under the equivalent range of light intensity levels from the sun (twilight, spanning from 1 Wm^{-2} to 0.001 Wm^{-2}) and the moon (moonlight, spanning from 0.001 Wm^{-2} to 0.00001 Wm^{-2}) (Regular et al. 2011). Nest arrivals bellow these ranges (< 0.00001 Wm^{-2}) were assumed as under 'darkness'.

1.3.2.2 Analysis of oceanographic conditions and foraging effort

To characterize local oceanographic conditions in the colonies surroundings, data on Chlorophyll-a concentration (hereinafter, CHL) was extracted from http://oceanocolor.gsfc.nasa.gov/ at a resolution of 0.04° (approx. 4 km), and Sea Surface Temperature from http://marine.copernicus.eu. at a resolution of 0.08° (approx. 8 km), as monthly night-time attributes for August-September of each study year, within a radius of 200 km around each breeding colony. The monthly CHL and SST attributes were then averaged for the study period of each year. Sea Surface Temperature anomalies (herein, SST anomaly) were computed by calculating the difference between the median peak of the variable for the mid-chick rearing period (August-September) and the observed average for the same period over 25 years of monthly climatological data (1993–2018). Differences in CHL and SST anomaly were analysed among years with one-way ANOVAs for each colony followed by post-hoc Tukey tests for multiple comparisons, using the ´aov´ and 'TukeyHSD' functions, respectively, in the R package ´stats´ (R Development Core Team 2020). Furthermore, foraging trips were discriminated by short versus long trips as a measure of the birds' effort to obtain food, and their respective proportion, duration and maximum distances from colony were also used as proxies for profitability of food resources around breeding colonies. Foraging trip duration corresponds to the time (in days) comprised between the departure and the return of an individual to the nest, whereas the maximum distance from colony (in kilometres) corresponds to the farthest location visited per foraging trip considered.

1.3.3 Patterns of nest arrival throughout the lunar cycle between years of contrasting oceanographic conditions

In order to understand if oceanographic stochasticity influenced the shearwaters' nest attendance patterns throughout the lunar cycle, linear mixed-effects models were considered for years of contrasting oceanographic conditions around each colony. In particular, years when CHL was significantly higher and SST anomaly was significantly lower were assumed as exceptionally profitable, while years with significantly lower CHL and significantly greater SST anomaly were considered impoverished. Therefore, separated models (assuming the pool of years with contrasting oceanographic conditions around each colony) were used to test for relationships between timing of nest arrival and moon fraction throughout the lunar cycle (Figure 2).

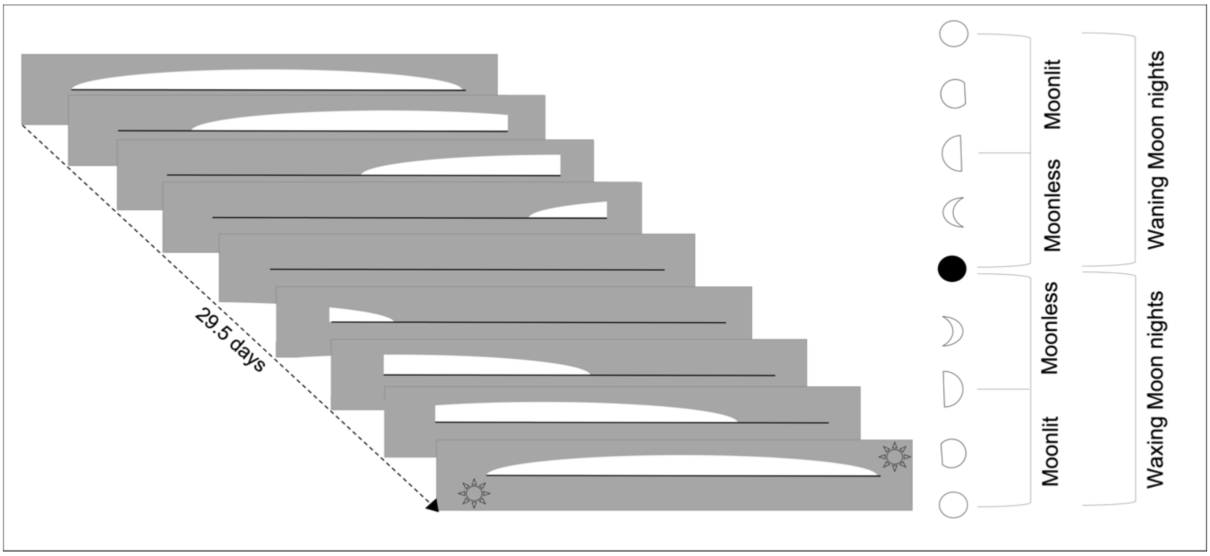


Figure 2 - Moon patterns throughout the lunar cycle, discriminated by waning and waxing moon nights, including moonlit or moonless nights. The new moon is displayed as a black circle. Different moonlight patterns emerge from waning or waxing moon nights (illustrated in white throughout the complete nights, i.e. after sunset and before sunrise), namely a growing period of darkness until moonrise over waning moon nights or a growing period of moonlight until moonset during waxing moon nights.

Moon fraction is the fraction of the lunar disk that is illuminated in each night, continuously changing from 1 in the full moon to 0 in the new moon nights (extracted for each night and study site location from http://aa.usno.navy.mil/data/docs/MoonFraction.php). Additionally, within a complete lunar cycle (29.5 nights), waning moon nights correspond to the set of 14/15 nights along which the moon fraction decreases from the full moon to the new moon (encompassing a growing period of darkness until moonrise), while during the 14/15 nights of waxing moon nights the moon fraction increases from the new moon towards the full moon (encompassing a growing period of moonlight until moonset) (Figure 2). Therefore, in order to discriminate the influence of waning and waxing moon phases throughout a complete lunar cycle, the moon fraction was included into the models as a fixed effect interacting with each set of these nights separately. The intercept for birds'ID was also integrated as a random effect to account for the hierarchical structure of the data (Bolker et al. 2009). Because timing of nest arrival did not follow normal distribution requirements, the linearity and the homoscedasticity of the residuals were achieved by using logarithmic transformations (Neter et al. 1996). Thus, a Normal variance distribution with an identity link function was used for timing of nest arrival in all models (Cameron and Trivedi 1998). The function 'lme' in the R package 'nlme' (Pinheiro et al. 2016) was used to perform linear mixed effects analysis (R Development Core Team 2020). Timing of nest arrivals and light intensity at burrow entrances (i.e. proportion of arrivals under twilight, moonlight and darkness) were plotted for waning and waxing moon nights between years of contrasting oceanographic conditions.

1.3.3.1 Analysis of nocturnal foraging activity

These analyses intended to investigate the influence of oceanographic conditions in the individuals’ behaviour at sea and how this relate with patterns of nest arrival throughout the lunar cycle. For this, nocturnal at-sea behaviour was characterized according to a binary discretization of the shearwaters’ tracking data in terms of velocity and turning behaviour, using the Expectation-Maximization binary Clustering (EmbC) algorithm for behavioural classification of movement data (Garriga et al. 2016). Tracking data based on 5 minutes intervals were subsampled into 10 minutes intervals so that differences in the GPS data resolution (Appendix A) would not bias characterization of turning behaviour. The EmbC enabled to categorize data-points into one of the following behavioural states: resting (i.e. low velocities and low turns), intensive search (i.e. low velocities and high turns), travelling (i.e. high velocities and low turns), and extensive search (high velocities and high turns). Only tracking positions within the time lag between sunset and nest entrance were considered in the analysis, as the proportion of time allocated per foraging trip for each specific behavioural category. Since intensive and extensive search are the most indicative behaviours of active foraging, these two categories were combined into a single behavioural class that was the target of our analyses. For comparative analyses of nocturnal at-sea behaviour, we considered nest arrivals after 1, 2 and 3 hours since sunset, in order to address potential variations in the individuals' foraging activity in relation to time spend at sea. A Kruskal-Wallis was used to test if variations in shearwaters’ nocturnal activity were related to changing patterns of nest arrival between years of contrasting oceanographic conditions, using the ´kruskal.test´ function in the R package ´stats´ (R Development Core Team 2020).

1.4 Results

1.4.1 Patterns of nest arrival in relation to annual variation in oceanographic conditions

Berlenga: Oceanographic data around Berlenga indicate that 2010 and 2014 were years of contrasting oceanographic conditions around the island (Table 1), with CHL presenting significantly lower values ($F_{8,369} = 2.59$, $P = 0.02$) and SST anomaly significantly higher values than those in all other years ($F_{8,167} = 2.34$, $P = 0.01$). Furthermore, birds seemed to exhibit greater relative foraging effort in 2010 and 2014, namely in terms of maximum and average duration of long foraging trips, including maximum distances from colony, and proportion of long trips in 2010 (Table 1).

Breeding birds attended the nests significantly earlier in 2010 than in all other years ($\chi2 = 192.05$, df = 8, $P < 0.001$), and arrived at the colony under significantly more intense light levels in 2014 than in the other years, with the exception of 2007 ($\chi2 = 289.7$, df = 8, $P < 0.001$) (Figure 3a, Appendix B). In 2010, breeding birds attended the colony under significantly more intense light levels than in 2012, 2015 and 2016 (Figure 3a, Appendix B). In particular, 2010 was the year when the greatest proportion of nest arrivals was under light levels equivalent to twilight (Figure 3a), while in 2007 and 2014 nest arrivals were mostly under moonlight (Figure 3a).

Corvo: The CHL was significantly higher in 2010 than in the other years ($F_{3,164} = 5.78$, $P = 0.001$), while SST anomaly was significantly lower in 2010 and 2015 ($F_{3,164} = 3.33$, $P = 0.02$). In 2010, shearwaters presented lower foraging effort in terms of proportion, maximum and average duration of long foraging trips (Table 1).

In terms of nest attendance patterns, nearly significant differences suggest that birds returned to the colony later in 2010 than in 2017 ($\chi2 = 7.35$, df = 3, $P = 0.06$), entering into the nests under significantly less intense light levels in 2010, when compared to 2007 and 2017 ($\chi2 = 29.17$, df = 3, $P < 0.001$) (Figure 3b, Appendix B). In particular, 2010 was the year when the lowest proportion of nest arrivals was under light levels equivalent to twilight (Figure 3a), while in 2007 and 2017 the greatest proportion of nest arrivals were under moonlight (Figure 3b).

Porto Santo: The CHL was significantly lower ($F_{3,164} = 3,11$, $P = 0.03$) and SST anomaly was significantly higher in 2011 than in the other years ($F_{3,164} = 2.89$, $P = 0.04$), and birds presented greater foraging effort in terms of maximum foraging trip duration and proportion of long foraging trips, including average foraging distance from colony during short trips (Table 1).

Cory’s shearwaters in Porto Santo did not present significant differences in timing of nest arrival between years ($\chi2 = 3.64$, df = 3, $P = 0.30$), and birds attended the nest under significantly more intense light levels in 2011 than in 2015 ($\chi2 = 9.44$, df = 3, $P = 0.02$) (Figure 3c, Appendix B). Among all, 2011 was the year when the greatest proportion of nest arrivals was under light levels equivalent to twilight and moonlight (Figure 3c).

Raso: The CHL was significantly lower in 2013 ($F_{3,164} = 5.69$, $P = 0.001$) and SST anomaly was significantly higher than in the others years ($F_{3,164} = 5.89$, P = 0.001), when birds seemed to exhibit greater relative foraging effort in terms of maximum duration of long foraging trips (Table 1).

Cape Verde shearwaters attended the nests significantly earlier in 2013 than in 2014 and 2015 (χ2 = 19.98, df = 3, P < 0.001), and returned to the colony under significantly more intense light levels in 2013 than in the other years (χ2 = 46.36, df = 3, P < 0.001) (Figure 3d, Appendix B). Among all years, 2013 was the only year when Cape Verde Shearwaters returned ashore under twilight (Figure 3d).

A full description of all parameters that varied significantly among years in terms of timing of nest arrival and light intensity at burrow entrances are shown in Appendix B.

Table 1 - Inter-annual patterns of oceanographic conditions and foraging effort of Cory’s and Cape Verde shearwaters: Environmental predictors - Chlorophyll-a concentration and Sea Surface Temperature anomaly within 200 Km from breeding colonies (mean ± SD); Foraging Trip Characteristics - minimum and maximum duration of foraging trips and proportion of short foraging trips (SFT; ≤ 4 days for Cory’s shearwaters and ≤ 3 days for Cape Verde shearwaters) and long foraging trips (LFT; > 4 days for Cory’s shearwaters and > 3 days for Cape Verde shearwaters), discriminated by duration and maximum distances from colony (mean values). Years when both SST anomaly and CHL differed significantly are highlighted in bold (P < 0.05) (* p<0.05; ** p<0.01; *** p<0.001). Study colonies of Cory’s shearwaters (*Calonectris borealis*) in Berlenga Island (Berlengas archipelago), Corvo Island (Azores archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

		Environmental predictors		Foraging trip characteristics		
		Chlorophyll-a concentration (CHL; mg m−3)	Sea Surface Temperature anomaly (SSTa)	Min/Max trip duration	Proportion of STF (average TD / average dist col)	Proportion of LTF (average TD / average dist col)
Berlenga	2007	0.67 ± 1.40	-0.36 ± 0.36	1/2	1.00 (1.12 / 26.5)	0.00 (- / -)
	2010	**0.27 ± 0.17***	**1.89 ± 0.75***	**1/13**	**0.89 (1.49 / 67.5)**	**0.11 (7.14 / 698.8)**
	2011	1.00 ± 2.34	1.35 ± 0.36	1/7	0.90 (1.87 / 77.9)	0.10 (5.75 / 242.8)
	2012	0.97 ± 2.71	1.24 ± 0.23	1/6	0.99 (1.46 / 47.9)	0.01 (6.00 / 315.8)
	2013	1.09 ± 2.72	- 0.65 ± 0.56	1/7	0.96 (1.51 / 67.8)	0.04 (6.00 / 366.9)
	2014	**0.56 ± 1.84***	**1.84 ± 0.60***	**1/9**	**0.96 (1.50 / 50.8)**	**0.04 (7.00 /448.7)**
	2015	1.11 ± 2.84	-0.21 ± 0.54	1/4	1.00 (1.43 / 47.46)	0.00 (- / -)
	2016	0.78 ± 1.50	- 0.78 ± 0.86	1/7	0.96 (1.63 / 49.9)	0.04 (5.67 / 136.9)
	2017	0.85 ± 1.42	- 1.09 ± 0.65	1/7	0.97 (1.54 / 71.1)	0.03 (5.67 / 428.3)
Corvo	2007	0.10 ± 0.03	0.30 ± 0.28	1/11	0.89 (1.16 / 70.7)	0.11 (7.33 / 611.6)
	2010	**0.22 ± 0.02 ****	**- 0.52 ± 0.33***	**1/9**	**0.95 (1.20 / 84.3)**	**0.05 (6.23 / 642.3)**
	2015	0.12 ± 0.02	-0.64 ± 0.61*	1/10	0.75 (2.00 / 239.4)	0.25 (7.00 / 664.7)
	2017	0.11 ± 0.02	0.90 ± 0.30	1/15	0.55 (1.95 / 266.1)	0.45 (8.47 / 953.1)
Porto Santo	**2011**	**0.02 ± 0.01***	**1.97 ± 0.23***	**1/15**	**0.69 (1.22 / 112.4)**	**0.31 (9.42 / 992.9)**
	2012	0.07 ± 0.01	1.32 ± 0.21	1/13	0.76 (1.26 / 61.56)	0.24 (11.67 / 1071.7)
	2014	0.07 ± 0.01	0.70 ± 0.13	1/8	0.91 (1.41 / 52.8)	0.09 (7.33 / 631.1)
	2015	0.08 ± 0.01	0.73 ± 0.21	1/6	0.95 (1.40 / 86.8)	0.05 (6.00 / 586.8)
Raso	**2013**	**0.07 ± 0.03****	**0.97 ± 0.12****	**1/17**	**0.84 (1.14 / 107.3)**	**0.16 (7.55 / 553.6)**
	2014	0.16 ± 0.07	0.06 ± 0.15	1/14	0.53(1.12 / 162.1)	0.47 (9.43 / 638.6)
	2015	0.2 ± 0.09	0.08 ± 0.23	1/12	0.86 (1.21 / 81.3)	0.14 (6.25 / 227.5)
	2017	0.16 ± 0.06	0.80 ± 0.24	1/13	0.81 (1.10 / 95.6)	0.19 (7.16 / 643.0)

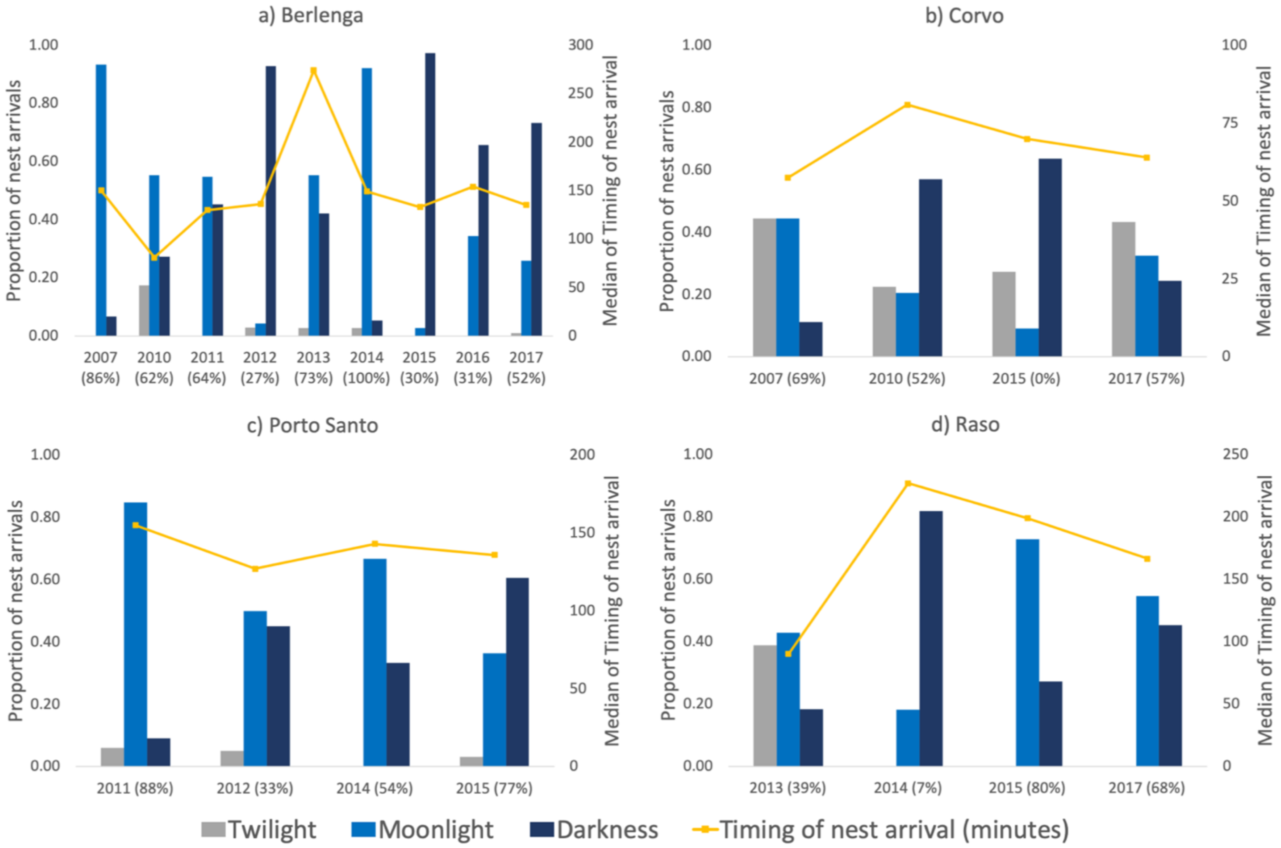


Figure 3 - Inter-annual patterns of shearwaters' nest attendance, discriminated by the timing of nest arrival after sunset (lines) and the proportion of nest arrivals (columns) under light levels from the sun (twilight; 1 Wm^{-2} to 0.001 Wm^{-2}), moon (moonlight; 0.001 Wm^{-2} to 0.00001 Wm^{-2}) and darkness (< 0.00001 Wm^{-2}). Percentage of moonlit nights (Figure 2) for each monitored year are displayed in brackets. Study colonies of Cory's shearwaters (*Calonectris borealis*) in (a) Berlenga Island (Berlengas archipelago), (b) Corvo Island (Azores archipelago) and (c) Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in (d) Raso Islet (Cape Verde archipelago).

1.4.2 Comparing patterns of nest arrival throughout the lunar cycle between years of good and poor oceanographic conditions

Atypical years for each colony were 2010 in Corvo (herein, good oceanographic conditions), 2010 and 2014 in Berlenga (herein, poor oceanographic conditions), 2011 in Porto Santo (herein, poor oceanographic conditions), and 2013 in Raso (herein, poor oceanographic conditions) (Table 1). Comparatively, 2007, 2015 and 2017 were classified as years of poor conditions around Corvo, while years of overall good oceanographic conditions were 2007, 2011, 2012, 2013, 2015, 2016 and 2017 at Berlenga, 2012, 2014, 2015 at Porto Santo, and 2014, 2015 and 2017 at Raso (Table 1). Therefore, in years of good oceanographic conditions, shearwaters in Berlenga, Corvo and Porto Santo did not change the timing of nest arrival during waning nights, adjusting burrow entrances with the onset of the nights, but significantly delayed nest arrival throughout waxing moon nights (i.e. as the moon fraction increased) (Figure 4 and Appendix C). In Raso, Cape Verde shearwaters delayed the nest arrival throughout waning and waxing moon nights (i.e. as the moon fraction decreased and increased, respectively), although burrow entrances were comparatively earlier in waning moon nights (Figure 4 and Appendix C). Under poor oceanographic conditions, shearwaters significantly attended the nests earlier throughout waning moon nights in Berlenga (i.e. as the moon fraction increased) (Figure 4 and Appendix C), while in Corvo, Porto Santo and Raso birds did not change the timing of nest arrival during waning nights (Figure 4 and Appendix C). In all colonies, shearwaters did not change patterns of nest arrival throughout waxing moon nights in years of poor oceanographic conditions (adjusting burrow entrances with the onset of the nights) (Figure 4 and Appendix C). Overall, breeding shearwaters tended to arrive into the nest mostly under darkness and moonlight in years of good oceanographic conditions (Figure 4), while in years of poor oceanographic conditions burrow entrances occurred mainly under light conditions equivalent to twilight and moonlight, regardless the typology of nights considered (Figure 4).

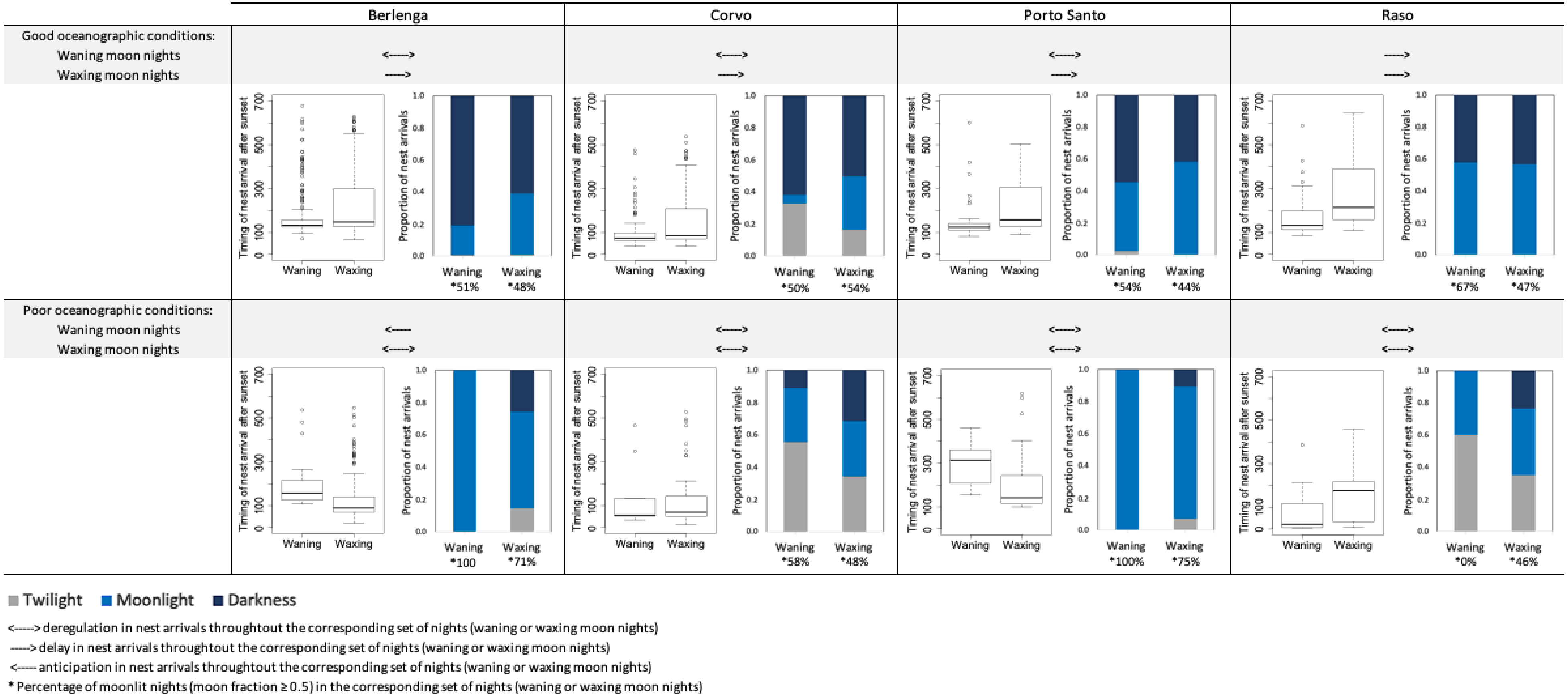


Figure 4 - Shearwaters' nest attendance patterns throughout the lunar cycle in years of good and poor oceanographic conditions around each studied colony: Regulation in nest arrivals throughout the corresponding set of nights (waning or waxing moon nights) (statistical outputs displayed in Appendix C); Variation of timing of nest arrivals after sunset in waning vs waxing moon nights (The lower and upper limits of each box represent the first and third quartiles, respectively, and the line inside each box represents the median. The bottom and top bars represent the minimum and maximum time of nest arrivals, respectively. Circles outside the first and third quartiles range are plotted as outliers); Proportion of nest arrivals discriminated by light levels from the sun (twilight; 1 Wm^{-2} to 0.001 Wm^{-2}), moon (moonlight; 0.001 Wm^{-2} to 0.00001 Wm^{-2}) and darkness (< 0.00001 Wm^{-2}) in waning and waxing moon nights. Percentage of moonlit nights for each typology of nights (waning and waxing moon nights; Figure 2) are marked with an asterisk. Study colonies of Cory's shearwaters (*Calonectris borealis*) in Berlenga Island (Berlengas archipelago), Corvo Island (Azores archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

1.4.2.1 Comparing nocturnal foraging behaviour in waxing moonlit nights between years of good and poor oceanographic conditions

While the previous results suggest that variations in local oceanographic conditions had little influence in the timing of nest arrival throughout waning moon nights, shearwaters consistently delayed nest arrivals during waxing moon nights in years of good oceanographic conditions but not in years of poor oceanographic conditions (Figure 4). These patterns indicate changes in the shearwaters nest attendance behaviour between years of contrasting oceanographic conditions associated with increasing moonlight exposure throughout waxing moon nights (Figure 2). Therefore, in order to understand the influence of oceanographic conditions in the individuals' behaviour at sea and how this relates with the previously identified changing patterns, we analysed the at-sea behaviour of individuals in waxing moonlit nights (Figure 2) between years of good and poor oceanographic conditions. The results show that, in Corvo, birds that spent at least three hours at sea after sunset were significantly more engaged in foraging activities in years of good oceanographic conditions (Table 2). In Raso, Cape Verde shearwaters that stayed at sea in the first two hours after sunset tended to significantly allocate more time foraging in years of good oceanographic conditions (Table 2). In Berlenga and Porto Santo, shearwaters did not present significant differences in at-sea behaviour between years of contrasting oceanographic conditions around the colony (Table 2).

Table 2 - Differences in the proportion of time allocated to active foraging (intensive and extensive search) within the time lag between sunset and nest entrance, between years of contrasting oceanographic conditions around each studied colony (Good: Good Oceanographic conditions; Poor: Poor Oceanographic conditions). These analyses comprehend variations in the individuals' foraging activity in relation to time spend at sea after sunset (nest arrivals after 1, 2 and 3 hours since sunset). Significant differences are highlighted in bold ($P < 0.05$) (* $p<0.05$; ** $p<0.01$; *** $p<0.001$). Study colonies of Cory's shearwaters (*Calonectris borealis*) in Berlenga Island (Berlengas archipelago), Corvo Island (Azores archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

Time at sea since sunset	Study Colonies	Proportion of active foraging per nest arrival	$\chi2$	df	P
more than 1 hour	Berlenga	Good (n= 102) = Poor (n = 60)	1.81	1	0.179
	Corvo	**Good (n= 55) > Poor (n = 11)**	6.62	1	0.010*
	Porto Santo	Good (n= 23) = Poor (n = 18)	2.87	1	0.090
	Raso	**Good (n= 96) > Poor (n = 15)**	4.23	1	0.039*
more than 2 hours	Berlenga	Good (n= 90) = Poor (n = 12)	0.27	1	0.603
	Corvo	**Good (n= 28) > Poor (n = 7)**	7.41	1	0.006**
	Porto Santo	Good (n= 19) = Poor (n = 12)	2.63	1	0.105
	Raso	Good (n= 88) > Poor (n = 15)	3.84	1	0.050
more than 3 hours	Berlenga	Good (n= 54) = Poor (n = 9)	0.83	1	0.361
	Corvo	**Good (n= 22) > Poor (n = 5)**	4.77	1	0.029*
	Porto Santo	Good (n= 14) = Poor (n = 7)	0.00	1	0.940
	Raso	Good (n= 67) = Poor (n = 11)	2.06	1	0.151

1.5 Discussion

1.5.1 Influence of oceanographic variability in the inter-annual patterns of timing of nest arrival and light intensity at burrow entrance

Annual changes in the shearwaters' timing of burrow entrance suggest a response strongly associated with inter-annual variations in oceanographic conditions around each colony. In particular, breeding birds attended the nests later in years associated with good oceanographic conditions, i.e. higher CHL concentration and cooler-water conditions (i.e. lower SST anomaly), when individuals exhibited a concomitant lower foraging effort. However, in years of poor oceanographic conditions (i.e. lower CHL concentration and warmer-water events), shearwaters returned to the colony earlier, mostly at dusk. Overall, nest arrivals under more intense light levels associated with twilight were markedly related to years of poor oceanographic conditions around breeding sites.

In fact, cooler-water temperature conditions associated with increased abundance of phytoplankton frequently implies greater abundance and availability of fish prey to marine top predators, such as seabirds (Bakun 2006; Druon et al. 2019). Therefore, variations in the marine productivity around breeding colonies have substantial influences on prey availability for Cory's shearwaters (Paiva et al. 2013), with direct consequences on the individuals' feeding behaviour, foraging effort and individual fitness (Paiva et al. 2010a,b; Ceia et al. 2014; Paiva et al. 2017). Under increased marine productivity around breeding colonies, shearwaters tend to forage at closer distances from breeding grounds, narrowing home ranges and consequently decreasing the duration of foraging trips (Granadeiro et al. 1998b; Magalhães et al. 2008; Paiva et al. 2010a; Paiva et al. 2015). Thus, better foraging conditions are often related with an overall increase in chick growth, reproductive success (Paiva et al. 2013, Ramos et al. 2003; Ramos et al. 2018) and adults' body condition (Paiva et al. 2017; Avalos et al. 2017).

According to our results, it seems that good foraging conditions around the colonies drive breeding individuals to spend more time at sea after sunset. For instances, the low marine productivity around Corvo (i.e. low CHL concentration and positive SST anomaly) indicate the prevalence of poor inter-annual foraging conditions for shearwaters breeding in this colony (Magalhães et al. 2008; Paiva et al. 2010a,b), which returned ashore relatively early over the monitored years. Yet, individuals tended to arrive into the nests later in 2010, when the marine productivity around Corvo was atypically high and breeding birds displayed a unimodal foraging strategy (mostly performing short foraging trips around the island) (Ceia et al. 2015), which is rarely adopted by oceanic populations that must cope with less profitable foraging conditions in the colony surroundings (Magalhães et al. 2008; Paiva et al. 2010a). In particular, differences in timing of nest arrival for Corvo were exclusively between 2010 and 2017, likely due to the overall low CHL concentration combined with the exceptional warmer SST that occurred in 2017 (markedly positive SST anomaly). On the contrary, in Berlenga, the inter-annual patterns of oceanographic conditions reflect the consistently good oceanographic conditions of this neritic colony (Paiva et al. 2010a,b; Paiva et al. 2017). Nevertheless, in 2010, Cory's shearwaters attended the nests significantly earlier, when a marked reduction in the abundance of pelagic prey fish around Berlenga triggered Cory's shearwater to increase the duration and distance of foraging trips, associated with the lowest breeding success recorded so far in this colony (Paiva et al. 2013; Paiva et al. 2017). The same pattern also occurred at Raso in 2013, when Cape Verde shearwaters returned ashore significantly earlier, and a remarkable increase in foraging trips duration and a decrease in chick body condition were related to unfavourable oceanographic conditions around Cape Verde (Ramos et al. 2018; Cerveira et al. 2020). At Porto Santo, the overall low marine productivity around this colony (i.e. low CHL concentration and positive SST anomaly) seems to indicate the prevalence of poor inter-annual foraging conditions, which may have not been sufficiently contrasting to reveal a clear changing pattern of timing of nest arrival among monitored years (see Avalos et al. 2017).

Overall, at a large spatial scale of the North Atlantic Ocean ranging from the Azores to Cape Verde, and considering the different oceanic contexts of each studied colony, the nest attendance patterns of shearwaters were strongly associated with changes in oceanographic conditions around breeding grounds. Since CHA, SST and patterns of shearwaters' foraging effort have been largely used as reliable proxies for resources profitability around breeding colonies (e.g. Paiva et al. 2010a,b; Paiva et al. 2013; Paiva et al. 2015; Paiva et al. 2017; Avalos et al. 2017; Ramos et al. 2015; Ramos et al. 2018), our results indicate that foraging conditions influenced the nest attendance behaviour of Cory's and Cape Verde shearwaters during chick rearing .

1.5.2 Effects of oceanographic and moonlight conditions in shearwaters' nest attendance patterns throughout the lunar cycle

Our results show that, in years of good oceanographic conditions, breeding birds in all studied colonies tended to adjust nest arrivals with the onset of waning moon nights (nights starting without the moon), but significantly delayed nest entrances throughout waxing moon nights (nights starting with the moon). These findings are consistent with several other studies showing that petrels and shearwaters regulate the timing of nest arrival to that of moonrise and moonset within the complete nights (Keitt et al. 2004; Bourgeois et al. 2008; Riou and Hamer 2008; Rubolini et al. 2015). However, the large proportion of burrow entrances under twilight and moonlight suggest that Cory's and Cape Verde shearwaters were little influenced by intense light levels at colonies. These results do not support the 'Predation Avoidance' hypothesis as a direct cause for the observed patterns, which is in line with recent studies showing that some shearwaters species do not avoid approaching their nests under moonlight (i.e. streaked shearwaters, *Calonectris leucomelas* and wedge-tailed shearwaters, *Ardenna pacifica*) (Van Tatenhove et al. 2018; Ravache et al. 2020).

On the other hand, because waxing nights entail a growing period of moonlight until moonset, nocturnal light intensity seemed to have implications in the at-sea behaviour of Cory's and Cape Verde shearwaters. In fact, several studies confirm that the lunar cycle influence the nocturnal foraging behaviour of pelagic seabirds (e.g. Phalan et al. 2007; Yamamoto et al. 2008; Dias et al. 2016; Ravache et al. 2020), including of Cory's shearwaters during non-breeding periods (Dias et al. 2012). According to Dias et al. (2012), Cory's shearwaters increase their flight activity on moonlit nights, yet a decrease in landing rate suggest a decline in foraging efficiency due to the reduced accessibility of prey on bright nights. Following this reasoning, less efficiency during the moonlit parts of the quarter-moon nights may drive birds to spend more time at sea (Klomp and Furness 1992), which can be a plausible explanation for the observed delay in nest arrivals throughout waxing moon nights. Conversely, an increase in foraging efficiency associated with a growing period of darkness until moonrise (throughout waning moon nights) may explain the early arrival of birds in this set of nights. It is however important to note that our understanding about the role of moonlight on prey accessibility, diet choices and foraging success of marine predators is still limited (Waap et al. 2017). Thus, the exact mechanisms underlying light-mediated patterns of seabirds' nocturnal foraging behaviour remain a challenging open question. The great consistency found in the obtained patterns still suggests that cloud cover, although not considered in our analyses, had a negligible effect in our results possibly due to the large data set included in this study.

Curiously, shearwaters did not delay nest arrivals with increasing moonlight exposure in years of poor oceanographic conditions around breeding sites. In this context, differences in the individuals' at-sea behaviour among colonies do not allow to establish a causal link between their foraging activities in waxing moonlit nights and patterns of nest arrival between years of contrasting oceanographic conditions. In particular, while shearwaters decreased foraging activity in years of poor conditions around Corvo and Raso, in Berlenga and Porto Santo breeding birds apparently did not change their behaviour at sea. These results also indicate that the mechanisms regulating the return of birds between years may not operate at the temporal scale considered in our analyses (i.e. between sunset and timing of nest arrival). In fact, since foraging decisions are likely to depend on whether animals self-feed or provision offspring (e.g. Ydenberg et al. 1994; Welcker et al. 2012), nest attendances may also vary according to the function of a foraging trip (e.g. Ydenberg 1994; Houston and McNamara 2014). Thus, inter-annual changes in patterns of nest arrival may reflect shifts in the individuals' provisioning strategies adjusted to the spatial distribution of resources around breeding sites (e.g. Ydenberg and Davis 2010). For instances, birds returning from distant self-feeding trips, which likely have fulfilled their energetic requirements in areas of enhanced profitability of resources (including gather food to the chick; Chaurand and Weimerskirch 1994a; Weimerskirch 1998), may be more prone to rapidly attend the nests at dusk. Therefore, more frequent returns from long trips in years of poor oceanographic conditions may explain the early arrival of birds to the nests, promoting a disruptive effect in attendances throughout waxing moon nights, as observed in our results. Conversely, high levels of synchrony in nest arrivals throughout waxing moon nights suggest that the main factor controlling the return of birds in years of good conditions was moonlight, a pattern that is more likely to emerge from foraging processes (i.e. provisioning decisions) at local scales (e.g. Gouhier et al. 2010). Overall, these results raise new questions about the individual-level foraging mechanisms regulating shearwaters' nest attendance decisions, a research field where clearly more investigation is needed. In particular, we highlight the importance of investigating the relative value of nocturnal foraging for breeding birds returning from functionally different foraging trips (i.e. self-feeding or chick provisioning trips), so that seabirds' nest attendance patterns and foraging behaviour under different moonlight conditions can be accurately interpreted from the standpoint of the 'foraging efficiency' hypothesis.

1.6 Conclusions

Based on a long-term GPS dataset from Cory's and Cape Verde shearwaters tracked across four breeding colonies in the Atlantic Ocean, this study shows that breeding birds adjusted nest attendance in relation to moonlight conditions throughout the lunar cycle. Despite the delay of nest arrivals throughout waxing moon nights, shearwaters did not avoid approaching their nests under moonlight suggesting that nocturnal light intensity has implications in the individuals' behaviour at sea. However, this pattern was not extensible to years of poor foraging conditions, when birds returned ashore early regardless of moonlight conditions. Combined, these results show that the nest attendance behaviour is mediated by moonlight in Cory's and Cape Verde shearwaters, a pattern that seems to be regulated by prevailing oceanographic and foraging conditions. We therefore highlight the role of nest attendance behaviour as a potential indicator of shearwaters' prey stocks around breeding colonies, strengthening the use of seabirds as bioindicators of marine environmental changes and fisheries related impacts (Einoder, 2009).

Chapter 2

Oceans of stimuli: an individual-based model to assess the role of olfactory cues and local enhancement in seabirds’ foraging behaviour

Photograph by Andrés de la Cruz 2019

2.1 Abstract

Oceans are extremely dynamic environments, which poses challenges for top predators such as seabirds to find food resources. Yet, seabirds evolved sensorial abilities (olfactory senses) along with complex behaviours (social information transfer through local enhancement) to improve foraging efficiency. Using the Cory's shearwater as a model species, we developed an individual-based model to explore the complementary role of different searching mechanisms (olfactory foraging and local enhancement) for the optimal foraging behaviour of pelagic seabirds during 1-day foraging trips around breeding colonies. Model outputs were compared with observed patterns of Cory's shearwaters distribution during local foraging trips. Also, the foraging efficiency of virtual individuals was analysed considering hypothetical scenarios of foraging conditions and densities of foraging individuals around breeding colonies. The results support the use of a combination of searching strategies by Cory's shearwaters, which produced representative patterns of space use from tracked individuals, including spatial foraging segregation of neighbouring sub-colonies. Furthermore, while the mechanisms underpinning local enhancement played a key role in mitigating sub-optimal foraging conditions, the use of olfactory senses conferred great adaptive foraging advantages over a wide range of environmental conditions. Our results also indicate a synergistic effect between the two strategies, which suggests that a multimodal foraging strategy is useful to forage in extremely dynamic environments. The developed model provides a basis for further investigation regarding the role of foraging mechanisms in the population dynamics of colonial animals, including the adaptive foraging behaviour of marine top predators to dynamic environmental conditions.

Keywords: *Calonectris borealis;* Density of conspecifics; Environmental scenarios; Foraging efficiency; Local enhancement; Olfactory search.

2.2 Introduction

Oceans are extremely heterogeneous and dynamic environments, in which oceanographic phenomena mediate trophic interactions at variable spatiotemporal scales (Weimerskirch 2007; Grémillet and Boulinier 2009). Consequently, finding food resources is challenging for top predators, such as seabirds, because prey distribution is patchy and unstable, and thus difficult to predict and locate. Under such circumstances, seabirds evolved remarkable sensory abilities that allow them to gain detailed knowledge of the marine environment (Nevitt 2008), which is particularly important during reproduction when breeding individuals must face spatial and temporal foraging constraints associated with chick rearing (Burke and Montevecchi 2009; Trevail et al. 2019). In particular, olfaction is among the most important senses thought to drive seabirds' navigation and foraging behaviour across the ocean (e.g. Cunningham et al. 2008; Nevitt et al. 2008; Wright et al. 2011; Gagliardo et al. 2013; Pollonara et al. 2015). Furthermore, seabirds may also detect prey directly using visual cues as private information, or indirectly through visual monitoring of conspecifics' behaviour as social information (e.g. Weimerskirch et al. 2010; Thiebault et al. 2014a,b; Boyd et al. 2016b). Nevertheless, there is still limited knowledge on how seabirds combine multiple strategies to locate food patches within apparently featureless seascapes and across variable foraging conditions.

The study of the interactions between searching strategies and resource availability requires a solid understanding of individual-level mechanisms underlying seabirds' foraging behaviour (Weimerskirch 2007; Thiebault et al. 2014a). In this context, ABMsse are extremely useful tools that allow to reproduce and test the mechanisms through which animals perceive, learn, and adapt to highly dynamic environments (Railsback 2001; DeAngelis and Mooij 2005; Grimm and Railsback 2005). ABMs undertake simulations where individuals respond to internal and external stimulus by seeking to maximize 'fitness', leading to the emergence of system-level properties (Grimm and Railsback 2005). In an attempt to make ecological modelling more rigorous and comprehensive, the pattern-oriented modelling approach was developed to recreate complex ecological and agent-based systems (Grimm and Railsback 2005; Grimm et al. 2005). Therefore, pattern-oriented modelling uses a set of observed patterns to compare, test, and validate ABMs, i.e. the closest the simulated patterns are to real data, the more accurate an ABM is considered (Grimm et al. 2005).

Cory's shearwaters present extraordinary olfactory abilities and rely strongly on their sense of smell to navigate over the pelagic realm (Gagliardo et al. 2013; Dell'Ariccia et al. 2014). Also, individuals of this species are often seen feeding in association with conspecifics, as well as other marine top predators such as cetaceans (Martin 1986), which lead us to hypothesize that Cory's shearwaters should exploit social information to target foraging grounds outside the colony (i.e. local enhancement hypothesis; Buckley 1997). Additionally, Cory's shearwaters form rafts (i.e. columns of birds laying on the sea surface) at open sea and off the colony before heading for the sea and in the end of the day, i.e. they leave the colony in the morning and come ashore strictly at dusk or during the night (Granadeiro et al. 1998b). Notably, the transference of social information also occurs through rafts (i.e. recruitment centre hypothesis; Richner and Heeb 1995), where birds can monitor the behaviour of conspecifics and take particular bearings based on foraging cues gained from successful foragers (e.g. Weimerskirch et al. 2010; Thiebault et al. 2014b). Nevertheless, social information transfer through rafts was not included in this study given the general lack of empirical knowledge on the functioning of rafts as potential information centres for shearwaters (Rubolini et al. 2015).

This study was directed to explore the role of olfactory search and local enhancement in seabirds' foraging behaviour during 1-day foraging trips around breeding colonies. For this, we used the Cory's shearwater as a model species and developed an ABM aiming to explore three main questions: (1) To what extent does the use of olfactory foraging and/or local enhancement reproduce realistic patterns of Cory's shearwater' foraging distribution and space use? (2) How does the use of olfaction contribute to the efficiency of individuals foraging in different environmental conditions? (3) What is the complementary role of olfactory information and local enhancement in the effectiveness of foraging across a gradient of foraging conditions around breeding colonies? Testing potential searching strategies used by Cory's shearwaters during local foraging trips, we expect that the developed modelling approach contribute to understand the mechanisms underlying the foraging behaviour of seabirds, including the complementary role of odour recognition and local enhancement in the individuals' foraging efficiency along a gradient of environmental conditions around breeding colonies.

2.3 Methods

To explore the role of olfactory search and local enhancement in seabirds' foraging behaviour, four hypothetical mechanisms were tested: H_0: virtual birds foraging without external cues (hereinafter, 'Uninformed Search'); H_1: virtual birds foraging according to an olfactory-based searching strategy (hereinafter, 'Olfactory Search'); H_2: virtual birds interacting with conspecifics through local enhancement (hereinafter, 'Local Enhancement'); H_3: virtual birds foraging according to an olfactory-based strategy and interacting with conspecifics through local enhancement (hereinafter, 'Olfactory Search with Local Enhancement'). Model outputs and performance were initially analysed through comparisons between real and simulated data in order to assess the mechanisms that best described patterns of Cory's shearwaters foraging distribution, using as baseline the data from Ceia et al. (2015). Also, the efficiency of virtual individuals using potential searching strategies was analysed considering three scenarios of foraging conditions, along with increasing densities of individuals. The model was developed using the software NetLogo 6.0.1. (Wilensky 1999). Full details on model conceptualization and assumptions are displayed in Appendix D, according to the overview, design concepts, and details (ODD) protocol (Grimm et al. 2010).

2.3.1 Model settings

The model was designed to recreate virtual Cory's shearwaters from two separated sub-colonies in Corvo Island (Azores, Portugal), foraging throughout a complete day during the chick rearing period (Ceia et al. 2015). Two types of conceptual entities were modelled: (1) internally homogeneous patches with 16 km^2 each (4 km × 4 km) that compose the virtual seascape and (2) mobile entities corresponding to Cory's shearwater virtual individuals (Appendix D, Sect. 2). The simulated environment included an area of 589 824 km^2 (768 km × 768 km) and the time unit was 5 min, representing the GPS temporal resolution of Cory's shearwaters tracking data (Ceia et al. 2015). Each simulation lasted 10h (120 time units), considered a reasonable period to recreate the average period during which Cory's shearwaters allocate foraging activities within a complete day cycle (Ramos et al. 2009; see also Paiva et al. 2013).

2.3.2 Conceptualization of movement behaviour and foraging mechanisms

2.3.2.1 Movement behaviour

Two ways of modelling animal movement were implemented, considering how individuals act on and react to the surrounding environment (Figure 5): (1) a correlated-random walk based on behavioural characteristics of Cory's shearwaters' movement (i.e. 'uninformed search') and (2) a biased correlated-random walk based on the correlated-random walk approach combined with the individuals' perception of seascape characteristics (i.e. 'Olfactory Search') or conspecifics' behaviour (i.e. 'local enhancement'), including the combination of both (i.e. 'olfactory search with local enhancement').

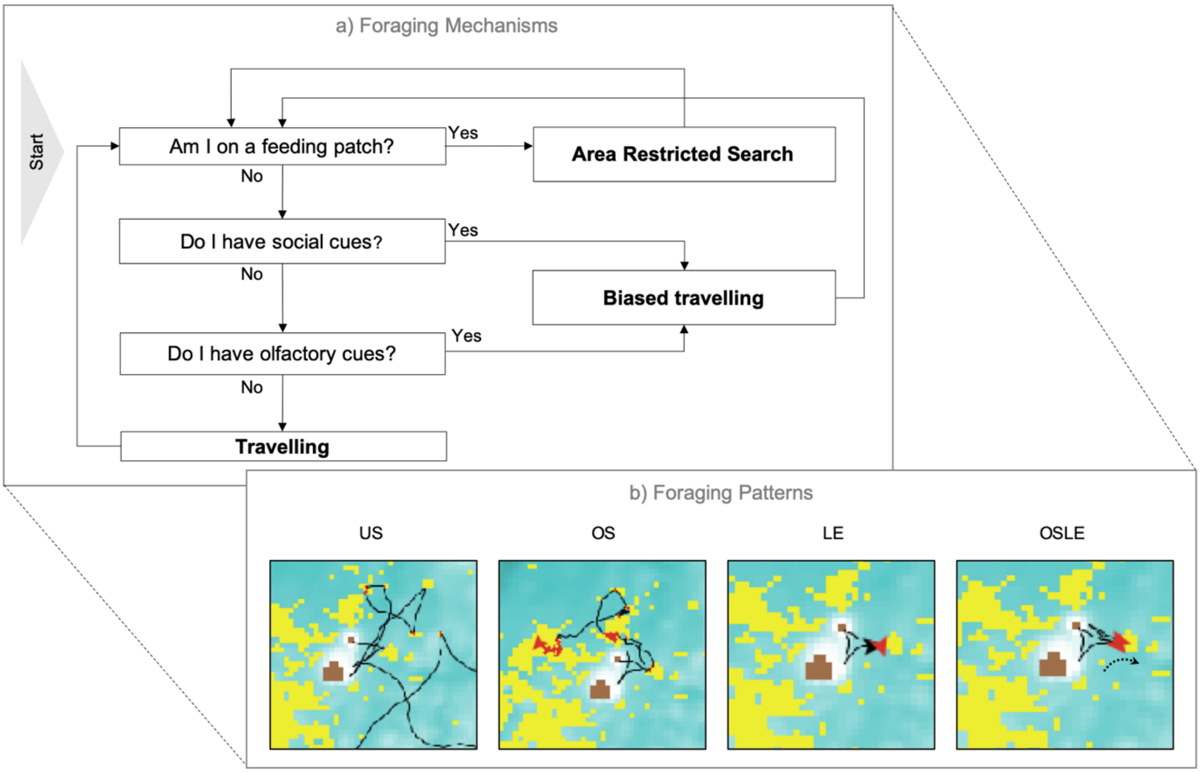


Figure 5 - a) Conceptual diagram of the virtual Cory´s shearwater' foraging mechanisms and b) emergent patterns of the individuals' foraging behaviour ('Uninformed Search' as US / 'Olfactory Search' as OS / 'Local Enhancement' as LE / 'Olfactory Search with Local Enhancement' as OSLE). Virtual birds assume a travelling mode while searching for resources throughout the seascape (a - Travelling; b - track in black and patches in blue) and perform ARS whenever they find a suitable feeding patch (a - Area Restricted Search; b - track in red and patches in yellow). When virtual birds perceive a feeding area by olfactory or social cues, a biased traveling is triggered towards the identified patch (a – Biased Travelling; b – OS, LE, OSLE); otherwise virtual individuals travel throughout the seascape solely relying on the information of the patch they are searching in (a – Travelling; b – US). Full details on Cory's shearwaters movement behaviour and foraging decisions are presented in Appendix D.

Geometric properties (i.e. velocity and turning behaviour) of real Cory's shearwater movements were extracted from 1-day foraging trips around Corvo, during August 2010 (Appendix D, Sect. 6). This data allowed assigning specific flight characteristics for two movement behaviours: Area Restricted Search (ARS) and Travelling (Appendix D, Sect. 7). In fact, ARS appears to be an individual reaction to changes in the resource availability, namely by reducing speed and increase turning rate (i.e. increasing residence time) as a response to increased productivity in a restricted area (Weimerskirch 2007). Contrarily, when travelling, individuals increase the flight velocity and reduce the turning angle, indicating lower foraging effort (Weimerskirch 2007). Therefore, a binary discretization of the shearwaters' real tracking data in terms of velocity and turning behaviour enabled to categorize data-points into ARS (i.e. low velocities and high turns) or travelling (i.e. high velocities and low turns), using the EmbC algorithm for behavioural classification of movement data (Garriga et al. 2016) (Appendix D, Sect. 6). The probability distribution of turning angles and flight velocity for each movement mode was then reproduced in the ABM according to randomly generated values within the obtained data distributions (Appendix D, Sect. 7). The movement of virtual birds was continuous over space and virtual birds were assumed to describe a travelling mode while searching for resources throughout the seascape (i.e. “flying” over unprofitable patches), whereas performing ARS behaviour whenever within suitable feeding patches (Figure 5). In this way, movement behaviours indirectly convey foraging efficiency since ARS increases residence time over more productive patches, while travelling minimizes the time spent over unprofitable areas. Furthermore, the time spent on profitable patches was drawn from the ARS properties of real Cory’s shearwaters, whose directional persistence (correlation between successive step orientations) expresses the individuals’ response to mechanisms acting at local scales (e.g. resources depletion) (Bartumeus et al. 2005).

2.3.2.2 Foraging mechanisms

While in the ‘Uninformed Search’ virtual birds solely relied on the information of the patch they were moving on (Figure 5), in the ‘olfactory search, ‘local enhancement’ and in the ‘olfactory search with local enhancement’ virtual birds were able to perceive external information (i.e. olfactory and social cues), adjusting their movement behaviour in response to the available information (i.e. biased travelling towards feeding areas) (Figure 5) (Appendix D, Sect. 7). For this, virtual birds perceived the seascape according to olfactory senses up to a maximum of 20 km ahead, assuming any wind direction on a 180° perception angle (based on wandering albatross evidence, i.e. Nevitt et al. 2008). Individuals also interacted with each other through visual contact (i.e. local enhancement), using visual acuity up to 10 km (based on data from Cape gannets *Morus capensis*; i.e. Thiebault et al. 2014a) on a vision radius of 148° ahead (based on data from Manx shearwater *Puffinus puffinus*; Martin and Brooke 1991). Since the detectability of feeding areas is presumably assessed at broader distances through olfactory cues, contrasting with the shorter distances based on visual information (Nevitt 2008), virtual birds tended to follow the behaviour of conspecifics whenever both olfactory and social stimuli were perceptible (Appendix D, Sect. 7). Although increasing aggregations of birds can enhance the detectability of larger clusters for other foragers (i.e. larger flocks are visible from larger distances) (Thiebault et al. 2014a), the structure of the network was not directly considered in the modelling procedure. Yet, the more virtual birds foraging in specific areas the greater the probability of other individuals to join the aggregation; thus, the effectiveness of local enhancement is indirectly influenced by larger flocks. Virtual shearwaters were also able to perceive land through visual perception, which they avoid over any other movement decision (Cory's shearwaters are rarely seen flying over land during the day; personal observation). Therefore, at departure from the colony, Cory's shearwaters adopted initial predefined heading (i.e. ranging from 45° to 225° and 135° to 315° in sub-colony A and B, respectively) that prevented individuals to assume bearings towards land when leaving the colony.

2.3.3 Environmental conditions and foraging efficiency

During August of 2010, Cory's shearwaters foraged mostly in areas around Corvo Island characterized by SST ranging from 23.5 to 24.2 °C, CHL ranging from 0.06 to 0.1 mg/m3, and bathymetry ranging from 730 and 2112 m (Ceia et al. 2015). Therefore, in order to recreate these conditions, bathymetry data were extracted from a grid of 0.01° (approx. 1 km) from https://www.ngdc.noaa.gov/mgg/global/global.html, and monthly average values of CHL and SST were downloaded from MODIS-Aqua (https://oceancolor.gsfc.nasa.gov/cgi/l3) at a spatial resolution of 0.04° (approx. 4 km), during August 2010. The obtained data layers were then imported into NetLogo and the availability of profitable patches was established by the respective thresholds of CHA, SST and bathymetry, according to Ceia et al. (2015) (hereinafter, baseline foraging conditions) (Figure 6) (Appendix D, Sect. 5).

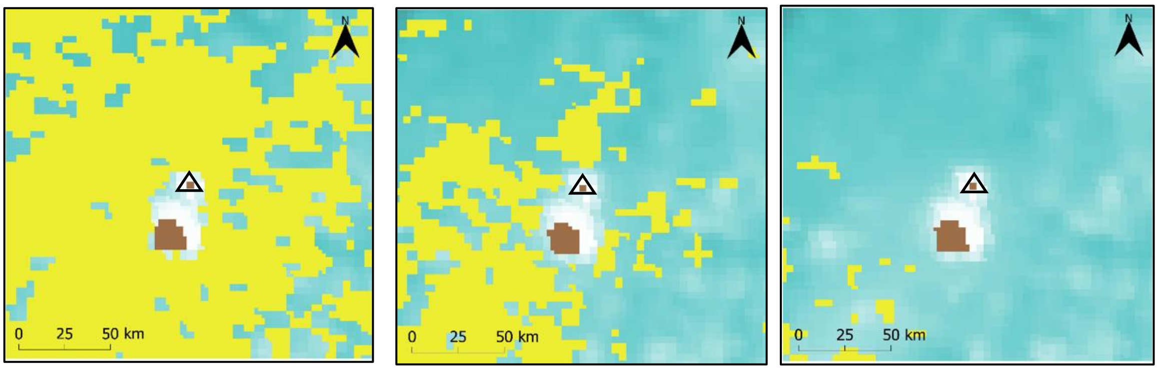


Figure 6 - Cory's shearwater habitat suitability around the Corvo Island, considering three scenarios of environmental conditions: Good foraging conditions (left), Baseline foraging conditions (centre) and Poor foraging conditions (right). Profitable feeding areas are represented in yellow, islands are represented in brown (the triangle indicates the location of the Corvo Island) and the background in blue illustrates bathymetry (lighter shades represent decreasing bathymetry). Full details on scenarios creation are presented in Appendix D.

Furthermore, to assess the effectiveness of searching mechanisms across a gradient of foraging conditions, two additional hypothetical scenarios were created, either richer in foraging patches (hereafter, good foraging conditions) or poorer in foraging patches (hereafter, poor foraging conditions) (Figure 6). For this, the percentages of profitable patches in the baseline scenario were calculated considering as denominator the total number of patches present in the seascape (36 864 patches). For demonstrative purposes, the scenarios of good and poor foraging conditions considered a relative increment or reduction of circa 50% in that percentage, respectively (Figure 6; Appendix D, Sect. 5). For each time unit spent on a feeding patch (i.e. within profitable areas), virtual individuals were programmed to gain 1 unit of energy; thus each bird was able to gain up to a maximum 120 units of energy after a day foraging at sea (hereinafter, individual energy score). The energy score (ES) is, therefore, assumed as a proxy of relative foraging efficiency, in terms of time spent on profitable areas, which depends on the combination between randomly generated movement patterns (see 'Movement behaviour') and the strategy used by the individuals in each scenario tested (see 'Foraging mechanisms').

2.3.4 Data analyses

2.3.4.1 Sensitivity analyses

A Global Sensitivity Analysis was performed to assess the sensitivity of the model outputs to changes in parameters, i.e. with + / − 10% variation of the respective values (Lee et al. 2015). A multiple regression analysis (based on Generalized Linear Models) was used to test for relationships between the energy score of individuals and parameters of movement behaviour (speed and turning angle of ARS and travelling), visual and olfactory acuity (visual acuity and perception angles of olfactory and visual stimuli), and the initial heading at departure from the colony. In particular, a s*tepwise* model selection procedure (using *the Akaike* Information Criterion) was applied to discriminate the magnitude and significance of the effect that each parameter caused in variations of energy gains after a foraging day. The statistical analysis was carried out using the *glm* and *step* functions in the stats R package (R Development Core Team 2017). Full details on sensitivity analysis are available in Appendix E.

2.3.4.2 Comparative analyses between real and simulated foraging patterns

Comparisons between real and simulated data were made to assess which hypothetical searching strategy produces the closest patterns observed in real tracked individuals. As a reference, we assumed the average oceanographic conditions around Corvo Island during August of 2010 (i.e. baseline foraging conditions) (see 'Environmental conditions and foraging efficiency'). For this, the response of 20 virtual birds in each sub-colony (the same number of individuals tracked in the study of Ceia et. al. 2015) was simultaneously considered throughout a foraging day, according to each searching strategy. The individuals were randomly selected from a total pool of 1000 virtual individuals per sub-colony (assuming breeders and non-breeders as both contribute to social information transfer), considering a population estimate of 200 breeding pairs for each sub-colony (Ceia et al. 2015) and 6000 breeding pairs for the whole Corvo Island (Oppel et al. 2014). Therefore, to compare real and simulated patterns, the following metrics were used (Ceia et al. 2015): (1) maximum distance from colony; (2) bearing from the most distant locations in relation to the colony; (3) geographic position (i.e. latitude and longitude) of foraging areas; (4) 25%, 50% and 75% foraging density areas (km^2), calculated by fixed kernel density (adehabitat package; h = 0.03°; grid = 500) (Calenge 2006). Individual information on virtual birds' identification, sub-colony, distance to nest, heading and movement behaviour (i.e. ARS or travelling) were extracted. ARS points were used to calculate areas of foraging (i.e. geographic position of foraging areas and fixed kernel density areas) (Ceia et al. 2015). Comparisons between real and simulated data were based on the mean values and standard deviation of the overall pool of foraging trips considered per sub-colony (i.e. 20 virtual individuals). The spatial patterns (i.e. 25%, 50%, 75% and 100% fixed kernel density areas) obtained for each colony and foraging mechanism ('Uninformed search', 'Olfactory search', 'Local enhancement' and 'Olfactory search with local enhancement') were also inspected. All spatial analyses were performed in ArcGis 10.5 (ESRI 2017).

2.3.4.3 Analyses of the efficiency of searching strategies across a gradient of foraging conditions

The individual foraging efficiency was analysed by considering a single sub-colony (i.e. sub-colony B). For each environmental scenario and foraging mechanism, 100 simulations were performed assuming an incremental number of virtual individuals in the sub-colony (i.e. 1, 10, 100 and 1000 individuals) (Figure 7).

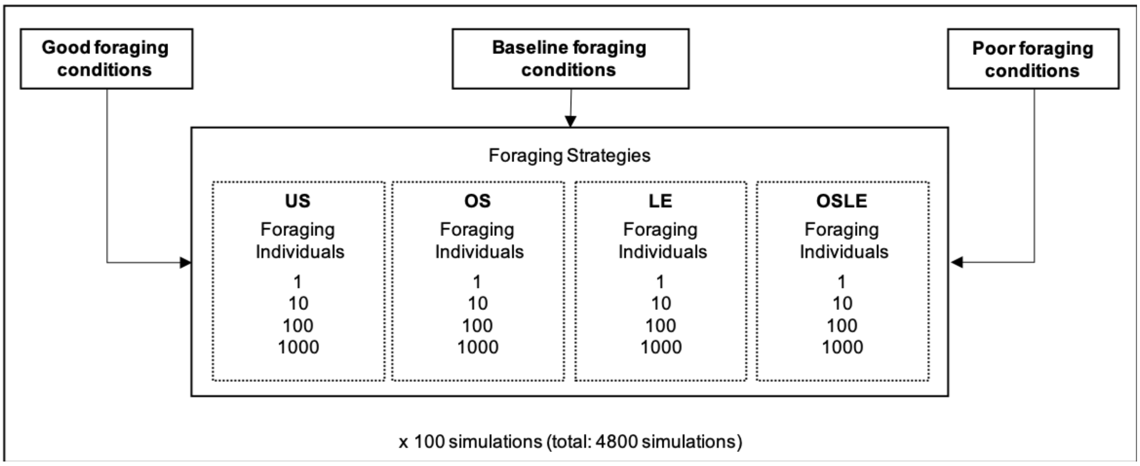


Figure 7 - Experimental design to compare the influence of foraging conditions (good/baseline/poor) and density of foraging individuals (1/10/100/1000 individuals) in the energy obtained by virtual individuals after a foraging day (median of energy score), according to different foraging mechanisms (‘Uninformed Search’ as US / ‘Olfactory Search’ as OS / ‘Local Enhancement’ as LE / ‘Olfactory Search with Local Enhancement’ as OSLE). For each experiment considered (e.g. 100 individuals foraging in a scenario of good foraging conditions, using the olfactory search), 100 simulations were performed (i.e. 48 experiments x 100 simulations = 4800 simulations).

Because outputs did not follow a normal distribution, the median of the individuals’ energy score was used in the analyses. The two-way Scheirer–Ray–Hare extension of the Kruskal–Wallis test (the non-parametric equivalent to the bifactorial ANOVA) (Sokal and Rohlf 1995) was then implemented to analyse whether foraging mechanisms interact with foraging conditions in influencing the energy score obtained by virtual individuals. As the results of different bird densities depended on the foraging mechanism tested (Figure 7), the number of individuals was nested within each searching strategy. Post-hoc analyses were performed using the Steel–Dwass–Critchlow–Fligner multiple-comparisons test (the non-parametric equivalent to the Tukey’s test) (Sokal and Rohlf 1995), in order to discriminate differences of energy (median of energy score) between individuals using different foraging strategies over contrasting environmental scenarios. The difference between the median of energy scores (Δmed_{ES}) and the percentage of energy scores ($\%_{ES}$) were, therefore, the metrics considered in the results. The percentage of energy scores was calculated by dividing the energy score of a virtual bird by the maximum possible units of energy scores (i.e. 120) (see ‘Environmental conditions and foraging efficiency’). The two-way Scheirer–Ray–Hare test was performed using the *scheirerRayHare* function in the rcompanion R package, and *post-hoc* multiple comparisons were analysed using the *dscfAllPairsTest* function in the PMCMR- Plus R package (R Development Core Team 2017).

2.4 Results

2.4.1 Sensitivity analyses

Results from the SRC sensitivity analyses indicate that speed of ARS and of travelling, visual acuity, and the perception angles of olfactory and of visual stimuli were key parameters that caused the main variations in the individuals' energy gains after a foraging day (Appendix E). On the contrary, the turning angle of ARS and of travelling, and the initial heading at departure from the colony did not have a significant influence in the response (Appendix E).

2.4.2 Performance of the simulated foraging patterns

Overall, virtual individuals reduced foraging areas and maximum foraging distances as they were able to perceive the surrounding environment through olfactory and/or social cues (Figure 8; Table 3). In particular, the 'local enhancement' and 'olfactory search with local enhancement' were the strategies that seemed to best reproduced the area of habitat use by Cory's shearwaters during local foraging trips around the Corvo Island (i.e. the same order of magnitude between real and simulated FKD areas, including less variability in the response) (Table 3). Furthermore, while local enhancement seemed to contribute for greater differences in the orientation of outbound headings between individuals from the two sub-colonies than the 'olfactory search' (Mean bearing, Table 3), a more prominent longitudinal segregation of foraging areas between neighbouring individuals was obtained when virtual birds tracked olfactory cues (Long ARS zones, Table 3). Consequently, according to the 'olfactory search with local enhancement', virtual individuals from sub-colony A foraged mostly towards the eastern area of the Corvo island, while individuals from sub-colony B targeted the western area (Figure 8). The spatial patterns of at-sea use by virtual birds were overall closer to those of real Cory's shearwaters when combining olfactory and social cues (i.e. FKD areas, Mean bearing and Long ARS zones, Table 3), which suggests that the 'olfactory search with local enhancement' is the strategy that presents more realism in recreating patterns of space use from tracked individuals (Table 3).

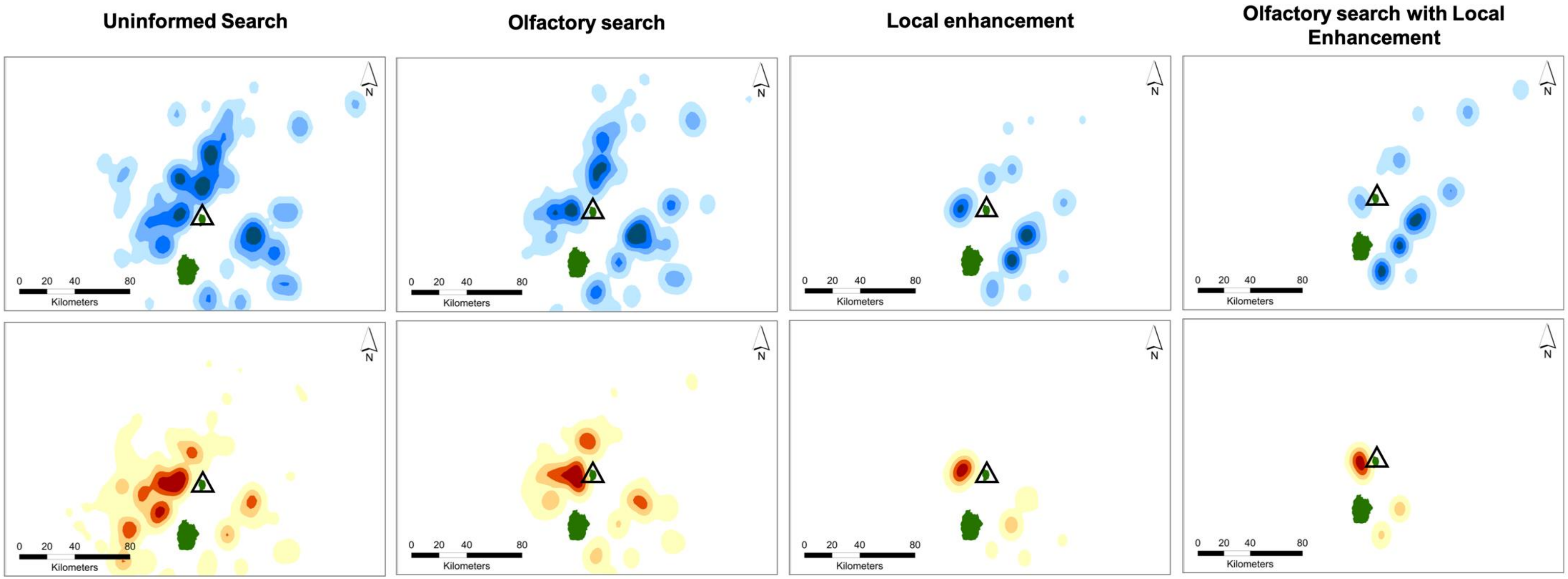


Figure 8 - Spatial distribution of virtual Cory's shearwaters from two sub-colonies (sub-colony A: upper panel; sub-colony B: lower panel) located in the Corvo Island (signed with the triangle), during local foraging trips (i.e. <1 day) in August 2010 (mid chick rearing), according to the 'Uninformed Search', 'Olfactory Search', 'Local Enhancement' and 'Olfactory Search with Local Enhancement'. Darker to lighter shades represent 25, 50, 75 and 100 % kernel densities, respectively.

Table 3 - Quantitative metrics of real (i.e. Data tracking) and simulated data (ABM simulated data, discriminated by the ‘Uninformed Search’, ‘Olfactory Search’, ‘Local Enhancement’ and ‘Olfactory Search with Local Enhancement’), per sub-colony (sub-colony A and B): maximum distance from colony, 25%, 50% and 75% foraging density areas, bearing from the most distant locations in relation to the sub-colony, and geographic position (i.e. latitude and longitude) of foraging areas. Values are presented as mean ± standard deviation.

	Data tracking		**ABM simulated data**							
	(Ceia et al. 2015)		**Uninformed Search**		**Olfactory Search**		**Local Enhancement**		**Olfactory Search with Local Enhancement**	
	Sub-colony A	**Sub-colony B**	**Sub-colony A**	**Sub-colony B**	**Sub-colony A**	**Sub-colony B**	**Sub-colony A**	**Sub-colony B**	**Sub-colony A**	**Sub-colony B**
Max distance (km)	62 ± 39		96 ± 87.0		54.2 ± 63.8		23.7 ± 17.3		27.4 ± 28.8	
75% FKD (km^2)	158 ± 63	135 ± 68	1424.6 ± 795.4	877.6 ± 642.7	937.4 ± 444.8	676.3 ± 608.9	335.4 ± 151.5	241.7 ± 129.3	360 ± 223.0	188 ± 30.0
50% FKD (km^2)	61 ± 32	53 ± 25	570.4 ± 339.2	325.2 ± 269	327 ± 177.9	224.4 ± 45.4	122.8 ± 36.4	103.2 ± 40.7	134 ± 63.1	88.3 ± 8.3
25% FKD (km^2)	23 ± 14	19 ± 8	174.8 ± 115.8	103.1 ± 81	100.2 ± 53.2	71.3 ± 44.8	43.8 ± 8.3	39.6 ± 10.8	47.5 ± 16.9	35.8 ± 3.0
Mean bearing	84.4 ± 38	251.2 ± 52.5	117.5 ± 87.5	176 ± 100	115.8 ± 66.3	170.3 ± 59	117.6 ± 85.8	179.7 ± 110.5	116.5 ± 43.5	190 ± 65.9
Lat ARS zones (° N)	39.8 ± 0.4	39.8 ± 0.4	39.6 ± 0.8	39.6 ± 0.3	39.6 ± 0.4	39.6 ± 0.4	39.6 ± 0.2	39.7 ± 0.1	39.6 ± 0.2	39.6 ± 0.1
Long ARS zones (° W)	−30.8 ± 0.4	−31.0 ± 0.4	-31.0 ± 0.5	-31.3 ± 0.3	-30.9 ± 0.3	-31.1 ± 0.2	-31.0 ± 0.2	-31.2 ± 0.2	-30.9 ± 0.2	-31.1 ± 0.1

2.4.3 Efficiency of searching strategies across a gradient of foraging conditions

2.4.3.1 Influence of foraging conditions

The results show that the energy obtained after a day foraging at sea (median of energy scores) was significantly influenced by the interaction between the searching strategy used by the individuals and the foraging conditions around the colony (Appendix F). In this context, regardless of the foraging mechanism used, virtual birds practically did not obtain energy scores (~ $0\%_{ES}$) when foraging in the scenario of poor foraging conditions (Figure 9; Table 4), but obtained overall highest energy scores (≥ $93.7\%_{ES}$) in the scenario of good foraging conditions using the ‘olfactory search’ and the ‘olfactory search with local enhancement’, as well as ‘local enhancement’ at densities of 1000 conspecifics (Figure 9; Table 4).

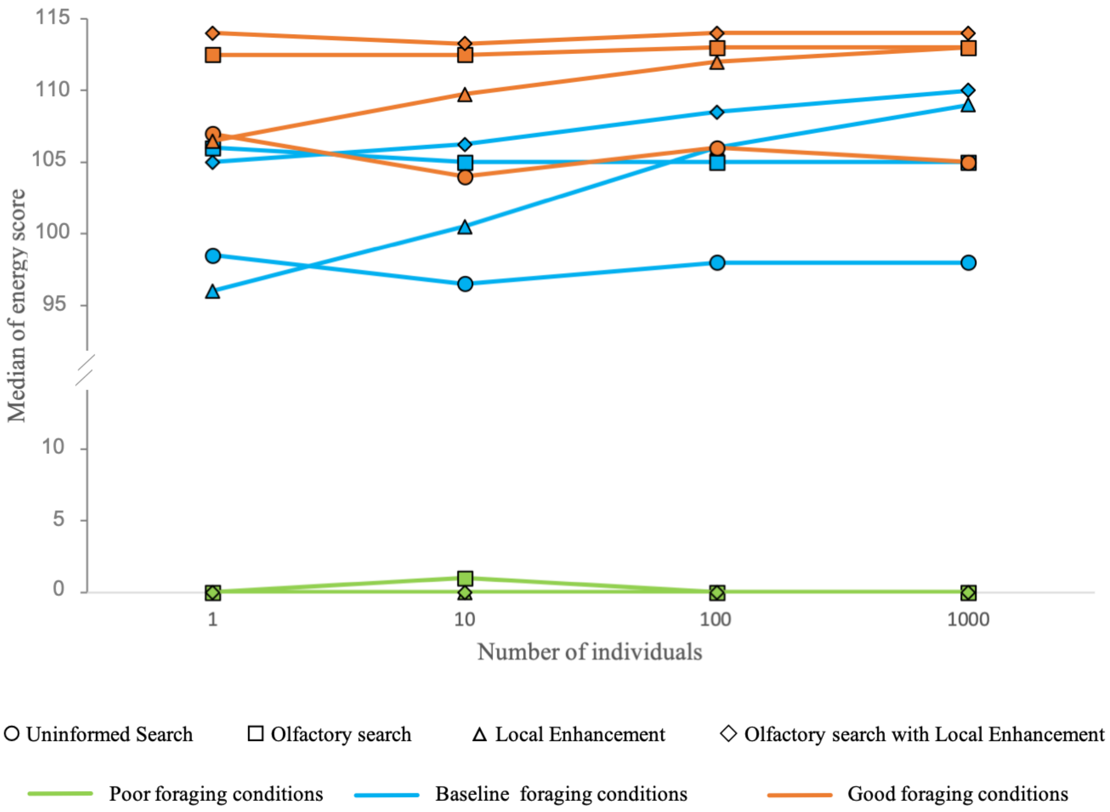


Figure 9 - Influence of foraging conditions and density of foraging individuals in the energy obtained by virtual individuals after a foraging day, according to different searching strategies. Results are shown as median values from 100 simulations (Median of energy score), according to the incremental number of virtual individuals in the sub-colony (Number of individuals). Foraging conditions around the breeding colony are represented in green (poor foraging conditions), blue (baseline foraging conditions) and orange (good foraging conditions), whereas foraging mechanisms are displayed as: ‘Uninformed Search’ (○), ‘Olfactory Search’ (□), ‘Local Enhancement’ (∆), ‘Olfactory Search with Local enhancement’ (◇).

Table 4 - Medians of energy score and respective percentages of energy score ($\%_{ES}$), given the maximum of 120 units of energy, from 100 simulations, taking into account the incremental number of virtual individuals (1, 10, 100 and 1000 individuals) per foraging mechanism ('Uninformed Search' as US, 'Olfactory Search' as OS 'Local Enhancement' as LE and 'Olfactory Search with Local Enhancement' as OSLE) in each environmental scenario considered (Good, Baseline and Poor foraging conditions).

		Number of virtual individuals							
Environmental scenario	**Foraging mechanism**	**1**		**10**		**100**		**1000**	
Good foraging conditions	**US**	107.00	89.17 $\%_{ES}$	104.00	86.67 $\%_{ES}$	106.00	88.33 $\%_{ES}$	105.00	87.50 $\%_{ES}$
	OS	112.50	93.75 $\%_{ES}$	112.50	93.75 $\%_{ES}$	113.00	94.17 $\%_{ES}$	113.00	94.17 $\%_{ES}$
	LE	106.50	88.75 $\%_{ES}$	109.75	91.46 $\%_{ES}$	112.00	93.33 $\%_{ES}$	113.00	94.17 $\%_{ES}$
	OSLE	114.00	95.00 $\%_{ES}$	113.25	94.38 $\%_{ES}$	114.00	95.00 $\%_{ES}$	114.00	95.00 $\%_{ES}$
Baseline foraging conditions	**US**	98.50	82.08 $\%_{ES}$	96.50	80.42 $\%_{ES}$	98.00	81.67 $\%_{ES}$	98.00	81.67 $\%_{ES}$
	OS	106.00	88.33 $\%_{ES}$	105.00	87.50 $\%_{ES}$	105.00	87.50 $\%_{ES}$	105.00	87.50 $\%_{ES}$
	LE	96.00	80.00 $\%_{ES}$	100.50	83.75 $\%_{ES}$	106.00	88.33 $\%_{ES}$	109.00	90.83 $\%_{ES}$
	OSLE	105.00	87.50 $\%_{ES}$	106.25	88.54 $\%_{ES}$	108.50	90.42 $\%_{ES}$	110.00	91.67 $\%_{ES}$
Poor foraging conditions	**US**	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$
	OS	0.00	0.00 $\%_{ES}$	1.00	0.83 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$
	LE	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$
	OSLE	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES}$	0.00	0.00 $\%_{ES,}$

Therefore, for each searching strategy, energy gains increased as the foraging conditions around the colony also improved (e.g. 1000 individuals: $OSLE_{poor}$ vs $OSLE_{baseline}$ Δmed_{ES} = 110.00, *p* value < 2.2e-16; $OSLE_{poor}$ vs $OSLE_{good}$ Δmed_{ES} = 114.00, *p* value < 2.2e-16; Appendix G). As virtual individuals were almost unable to find resources under poor foraging conditions independently of the mechanism used, the baseline scenario and the scenario of good foraging conditions were determinant to compare the efficiency of each searching strategy in relation to changing foraging conditions around the colony.

2.4.3.2 Effectiveness of searching mechanisms

Olfactory search Individuals using the 'olfactory search' gained more energy than individuals unable to perceive the surrounding environment (i.e. 'uninformed search'), independently of the foraging conditions around the colony (e.g. 100 individuals: $US_{baseline}$ vs $OS_{baseline}$ Δmed_{ES}=7, *p* value < 2.2e-16; US_{good} vs OS_{good} Δmed_{ES} = 7, *p* value < 2.2e-16; Appendix G) (Figure 9; Table 4). Also, virtual birds tracking olfactory cues in the baseline scenario were able to obtain similar energy of that gained by individuals using the 'uninformed search' in the scenario of good foraging conditions (e.g. 100 individuals: US_{good} vs $OS_{baseline}$ Δmed_{ES}=1, *p* value=0.27; Appendix G). Overall, differences in gains of energy between individuals using the 'uninformed search' and the 'olfactory search' were similar for the scenarios of baseline and good foraging conditions (Figure 9; Table 4).

Local enhancement Virtual birds tracking only social cues ('Local Enhancement') were dependent on higher densities of conspecifics to increase foraging efficiency above levels attained by individuals foraging according to the 'uninformed search' (e.g. 10 individuals: $US_{baseline}$ vs $LE_{baseline}$ Δmed_{ES} = 4, *p* value = 0.15; 100 individuals: $US_{baseline}$ vs $LE_{baseline}$ Δmed_{ES} = 8, *p* value < 2.2e-16; Appendix G) (Figure 9; Table 4). At relative high density of conspecifics (i.e. 1000 individuals), virtual birds relying solely on local enhancement in the baseline scenario tended to those obtained by birds relying on olfactory and social cues (~92%$_{ES}$; Figure 9; Table 4), but presented a similar foraging efficiency to that of individuals using the 'olfactory search' in the scenario of good foraging conditions (~ 94%$_{ES}$; Figure 9; Table 4).

Olfactory search with local enhancement Although virtual individuals using the 'olfactory search with local enhancement' were dependent on higher densities of conspecifics to increase foraging efficiency above levels attained by individuals using the 'olfactory search' (e.g. Baseline foraging conditions: $OS_{10individuals}$ vs $OSLE_{10individuals}$ Δmed_{ES} = 1.25, *p* value = 0.69; $OS_{100individuals}$ vs $OSLE_{100individuals}$ Δmed_{ES} = 3.5, *p* value < 2.2e-16; Appendix G) (Figure 9 and Table 4), the greatest differences in energy gains between virtual birds using these two strategies ('olfactory search' or 'olfactory search with local enhancement') were obtained in the scenario of baseline foraging conditions (1000 individuals: $OS_{baseline}$ vs $OSLE_{baseline}$ Δmed_{ES} = 5, *p* value = < 2.2e-16; OS_{good} vs $OSLE_{good}$ Δmed_{ES} = 1, *p* value < 2.2e-16; Appendix G) (Figure 9; Table 4). Furthermore, independently of the foraging conditions around the colony (either in baseline and good foraging conditions), virtual birds gained more energy when olfactory and social information were combined, than when used separately (Figure 9 and Table 4). All results of the Steel–Dwass–Critchlow–Fligner multiple comparisons are available on Appendix G, including differences between medians of energy scores (Δmed_{ES}).

2.5 Discussion

2.5.1 Searching mechanisms of Cory's shearwaters foraging behaviour

Our results suggest increased realism in reproducing real patterns of Cory's shearwater' foraging distribution as virtual individuals used external sources of information to detect profitable foraging patches. In fact, as the individuals' perception increased through olfactory senses and local enhancement, virtual birds tended to find resources in narrower ranges closer to breeding colonies, thus likely maximizing net energy gains for the lowest energy costs (e.g. Thiebault et al. 2014b). Furthermore, the longitudinal segregation of foraging areas by individuals from neighbouring sub-colonies was more pronounced as virtual birds were able to track olfactory cues. It is important to note that the initial heading taken by birds at departure from the sub-colonies was established according to the same predefined distributions in all foraging mechanisms. Despite these similar initial conditions, virtual birds unable to perceive external stimuli or relying only on local enhancement tended to overlap in foraging areas. Thus, the heading taken by virtual birds at departure from the colony did not seem to influence the segregation of foraging areas among neighbouring individuals. Instead, the tracking of olfactory scent cues since the colony departure seemed to guide virtual birds along a bearing perpendicular to the coastline, thus likely influencing individuals to forage in areas closer to their own colony than to any other. In fact, Padget et al. (2017) suggests that Scopoli's shearwaters (*Calonectris diomedia*) use olfactory information since the outbound sections of their foraging trips, as individuals deprived of their sense of smell (i.e. anosmic birds) became significantly more coastal upon departure from colony. A directional bias on a trajectory consistent with the general orientation of the breeding site also supports colony-specific foraging areas (e.g. Boyd et al. 2002; Robson et al. 2004), including for Cory's shearwaters (Ceia et al. 2015). However, the consistency of foraging routes at departure from colonies has been attributable to local habitat structure and previous foraging experience (Bonadonna et al. 2001; Robson et al. 2004), the latter not included in our modelling simulations. Also, spatial segregation is observed in species not considered particularly endowed with olfactory abilities (e.g. Cecere et al. 2018) and, therefore, other mechanisms should contribute to this geographic separation, probably as an adaptation to minimize intraspecific competition for resources (diplomacy Hypothesis; Grémillet et al. 2004). This may be the case of local enhancement that reinforced differences in the orientation of searching direction between virtual individuals from neighbouring sub-colonies. In fact, spatial segregation is consistent with the occurrence of social information transfer between individuals of the same sub-colony (e.g. Cecere et al. 2018; Jones et al. 2018). Specifically, local enhancement and the transfer of information at the colony are thought to be the most important mechanisms generating and maintaining specific foraging areas shared by individuals of the same colony (Wakefield et al. 2013). In this perspective, Cory's shearwater may also use rafts off the colony to obtain public information concerning feeding patches location, as noted in the "Introduction". For instance, some individuals may rely on short-term recall to exploit predictable feeding areas around the island, while conspecifics on rafts may gather information on food patches location based on the direction taken by these birds (e.g. Weimerskirch et al. 2010). Interestingly, Wakefield et al. (2013) used ABMs to show that memory and social information transfer off the colony and at sea produce a significant reduction in overlap between colony utilization distributions of Gannets (*Morus bassanus*). The exchange of social information may still occur at nest sites, enabling individuals to associate with successful conspecifics at departure for a new foraging trip (e.g. Waltz 1987; Wright et al. 2003; also see Burger 1997). Overall, despite the uncertainties about the mechanisms influencing the foraging behaviour of Cory's shearwaters, our results suggest that odour recognition and local enhancement likely underlie optimal foraging for shearwaters, which is in line with findings from several other studies (e.g. Nevitt et al. 2008; Thiebault et al. 2014a,b; Boyd et al. 2016b; Padget et al. 2017).

2.5.2 Efficiency of seabirds' searching strategies across a gradient of foraging conditions

The environmental scenarios considered were designed to simulate a gradient of foraging conditions that, in the absence of direct prey data fields around Corvo Island, were assumed to create distinct scenarios for prey abundance and distribution based on proxies for marine productivity (i.e. CHA, SST, and bathymetry). In fact, variations in the marine productivity around the breeding colonies have substantial influences on prey availability for Cory's shearwaters (Paiva et al. 2013), with direct consequences on the individuals' spatial distribution, feeding behaviour, and fitness (Paiva et al. 2010a,b; Ceia et al. 2014). Our results, therefore, suggest that, given the range of foraging conditions simulated in this study, the most determinant factor influencing the foraging efficiency of virtual birds was the availability of foraging areas around the colony, which suggests that resources are a key limiting factor for seabirds' foraging efficiency (e.g. Burke and Montevecchi 2009). Consequently, when facing a sharp decrease in the profitability of resources (scenario of poor foraging conditions) virtual individuals were unable to find resources regardless of the use of more sophisticated mechanisms, indicating that the olfactory-based foraging and local enhancement can only be effective above a minimum threshold of food availability. In such circumstances, the inability to cope with foraging conditions around the colonies should drive breeding individuals to enlarge foraging trips to exploit areas with enhanced marine productivity over seamounts and frontal regions, where resources are more stable and, therefore, predictable (Paiva et al. 2010b).

When resources are readily available in the colonies' surroundings, our results indicate that the olfactory search confers great adaptive foraging advantages over a wide range of environmental stochasticity. In fact, seabirds, and especially tube-nosed procellariforms (i.e. albatrosses, petrels and shearwaters), have evolved extraordinary well-adapted olfactory systems in response to the selective pressures imposed by the pelagic environment (Nevitt 2008; Van Buskirk and Nevitt 2008). Therefore, an odour-oriented search not only allowed virtual birds to maximize energy gains when compared with individuals unable of perceive the environment, but also enabled them to increase energy gains both in intermediate (baseline) and good foraging conditions in the same proportion. On the other hand, the effectiveness of local enhancement was influenced by variations in the density of conspecifics and foraging conditions around the breeding colony. This is in agreement to the local enhancement hypothesis, showing that a decrease in density of conspecifics impairs the chances of the mechanisms of social information transfer to be effective (Thiebault et al. 2014a,b; Boyd et al. 2016b). Furthermore, local enhancement had a less prominent influence on the foraging efficiency of individuals for the scenario of good foraging conditions. This suggests that, when resources are more abundant or easier to find, birds may be less dependent on each other to gain additional information for the location of feeding patches (Thiebault et al. 2014b; Boyd et al. 2016b). On the contrary, under sub-optimal foraging conditions (baseline foraging conditions), local enhancement seemed to play a key role by allowing virtual birds solely relying on social cues to increase foraging efficiency to a greater level than that of an exclusively olfactory search. Interestingly, recent research showed that anosmic Scopoli's shearwaters dramatically impaired homing ability, although a shift to visual foraging based on local enhancement likely contributed to overcome the lack of olfactory stimuli, not significantly affecting foraging success (Padget et al. 2017). Our results support these findings by demonstrating that, in the baseline scenario, 'virtual anosmic' birds (i.e. that rely uniquely on local enhancement) in the presence of relative high densities of conspecifics were able to increase energy gains to similar levels of that obtained by birds that combined olfactory and social information. It is, however, important to note that increased competition and accelerated resource depletion in larger seabird aggregations were not considered in our simulations and, therefore, the effectiveness of local enhancement can be less valuable in real contexts of rapid depletion through competition (Boyd et al. 2016b).

Since the olfactory search is presumably an innate mechanism of seabirds' perception, it is not reasonable to dissociate its role from the individuals' whole foraging behaviour. In fact, our results indicate a synergistic effect between olfactory foraging and local enhancement, as the integration of both mechanisms was more profitable than each separately, as well as greater than the balance (arithmetic mean) of their respective contributions. Both strategies should, therefore, jointly contribute to increase the probability of successful encounters with feeding opportunities (e.g. Mardon et al. 2010), probably because seabirds use olfaction to identify profitable patches at long distances and then rely on visual stimuli to detect prey (Nevitt 2008). Also, because the effectiveness of social information transfer is driven by either greater population densities (Thiebault et al. 2014a; Boyd et al. 2016b) or spatio-temporal synchronization of individuals (Jovani and Grimm 2008), an olfactory-based strategy may increase the efficacy of local enhancement by concentrating individuals in the same profitable grounds. The interpretation of our results, therefore, suggest that olfactory and visual cues should together activate the central cognitive mechanisms involved in seabirds' foraging behaviour. In fact, procellariforms present remarkable olfactory neuroanatomy that provides unique physiological and sensory abilities to successfully forage in the open ocean (Corfield et al. 2015), where wind fields help detecting productive patches (Nevitt et al. 2008; Abolaffio et al. 2018). Thus, olfactory senses should allow to build cognitive maps on the basis of odours that individuals can physiologically detect, such as the dimethyl sulphide produced by phytoplankton that is naturally associated with marine productivity (Nevitt and Bonadonna 2005; Dell'Ariccia et al. 2014). Likewise, increasing evidence points to sensitivity to dimethyl sulphide by non-procellariform seabirds such as penguins (Spheniscidae), which although considered visual hunters also track scent cues both at sea and on land (Cunningham et al. 2008; Wright et al. 2011). Nevertheless, as olfactory capabilities have evolved to meet the specific sensory demands of an ecological niche or behavioural adaptation, its importance should vary among seabird species (Corfield et al. 2015). On the other hand, the cognitive search image that seabirds probably use for local enhancement is oriented towards the behaviour of other predators (Tremblay et al. 2014), which is certainly favoured by their colonial behaviour and conspicuousness around breeding colonies (Evans et al. 2016). Therefore, while olfactory and visual stimuli are the probable key drivers for the cognitive representations of the external world that guide seabirds' orientation and navigation (Van Buskirk and Nevitt 2008), the demands of its highly dynamic marine environment should create an adaptive need for the expansion of their cognitive skills (e.g. imitation, learning and memory). In this way, individuals evolved foraging strategies that provide the most benefit for the lowest energy cost, thus maximizing individual fitness (Optimal foraging theory; Emlen 1966; Mac Arthur and Pianka 1966). Overall, our study suggests that the sensory pathways leading seabirds to explore and/or detect prey are triggered by multiple foraging stimulus, which used in combination allow to maximize net energy gains and thus confer adaptive advantages to forage in dynamic environments.

2.5.3 Future modelling directions

Using the Cory's shearwaters as a model species, the developed ABM allowed to address the comparative and complementary role of local enhancement and olfactory search in the optimal foraging behaviour of seabirds during local trips around breeding colonies. Our modelling approach is also a useful contribution to explore the influence of environmental stochasticity in the individuals' foraging behaviour at multiple spatio-temporal scales, and consequently for individual fitness and breeding performance (e.g. Trevail et al. 2019). In fact, upon appropriate conceptualization and parameterization and the integration of dynamic and stochastic oceanographic conditions, our model design can be extended to the entire breeding season in order to investigate the role of foraging behaviour in the breeding population dynamics of colonial seabirds. In particular, parametrization in terms of the individuals energetics (e.g. energetic gain from prey and costs of specific activities such as foraging) and time-activity budgets (e.g. foraging allocation decision rules) can lead to the emergence of variable foraging efficiency with consequences on trip duration, net energy intake, chick provisioning rates, breeding success and, ultimately, population dynamics. Also, the integration of additional mechanisms of foraging behaviour such as those relying on private information from short-term recall and memory, will allow to better understand how individuals employ a mixture of searching mechanisms to cope with resource profitability at variable spatio-temporal scales (e.g. short vs long foraging trips). Our model can still be used as a useful base to explore the role of rafts as potential information centres for Cory's shearwaters, by including the transference of social information at the colony in the modelling procedure. Overall, our modelling proposal can contribute to assess how the combined behavioural, social and life-history traits may influence the ability of seabirds to cope with long-term environmental changes. This is especially important in the context of the ongoing decline in oceanic primary productivity (Behrenfeld et al. 2006) triggered by global climatic change (Grémillet and Boulinier 2009). Therefore, predicting the consequences of long-term changes in the abundance and distribution of target species, and anticipating the potential causes of such decline in the future, may be crucial in the present to inform the design and implementation of conservation measures more effective in the long term.

Chapter 3

Mechanisms of parental behaviour and cooperation in chick provisioning decisions by a long-lived seabird: insights from a dynamic model with Cory's shearwaters

Photograph by Rita Bastos 2019

3.1 Abstract

Understanding the mechanisms driving the allocation of foraging effort by seabirds is essential to comprehend parental behaviour during reproduction. Using the Cory's shearwater as a test-species, we developed a dynamic model to explore the provisioning dynamics of long-lived seabirds during chick rearing, considering physiologic constraints and behavioural decisions of breeding pairs. We conceptualized different hypotheses regarding potential mechanisms involved in the individuals foraging-allocation decisions, assuming sequential adaptive compromises among the three family members (the focal bird, the chick and the partner). We also simulated changes in local foraging conditions to test whether the optimal solutions to these decisions change along a gradient of resources availability. Simulation results captured realistic variations in reproductive effort by Cory's shearwaters under contrasting environmental conditions, supporting the idea that parental investment is shaped by local prey availability. The outputs also suggest that the ability to regulate provisioning according to the chick's needs allows parents to minimize the cost of reproduction under better foraging conditions. In addition, a full cooperative strategy enabled parents to maximize the survival of their chick while minimizing energetic costs to themselves, buffering the effects of sub-optimal environmental conditions. Nevertheless, under severe scarcity of resources, the challenge of self-maintenance seemed to impair their ability to regulate chick provisioning according to the remaining family members, indicating that parental decisions may be flexible responses to local foraging conditions. The developed model contributed to investigate mechanisms of seabirds parental behaviour, providing a starting point for the integration of more detailed components with potential of application to other species and environmental contexts.

Keywords: adults' body condition; *Calonectris borealis*; foraging conditions; life-history traits; pair collaborative behaviour; system dynamics.

3.2 Introduction

Among pelagic seabirds, procellariforms (albatrosses, petrels and shearwaters) display extended parental care (around 6 months) to one chick from a single annual nesting attempt (Warham 1990). Despite their efforts to raise their offspring successfully, balancing reproductive investment with the maintenance of their own survival may be challenging (Stearns 1992; Ydenberg et al 1994). This occurs mainly when resources around the colonies are limited and breeding birds must admit lowering body condition in order to ensure frequent food delivery to their nestlings (Chaurand and Weimerskirch 1994b; Weimerskirch 1998; Weimerskirch and Cherel 1998). Under such circumstances, they adopt a dual-foraging strategy, alternating local forays mainly to capture prey for their chicks, with long trips towards areas of enhanced marine productivity for self-feeding and maintenance of body condition (e.g. Weimerskirch 1998; Congdon et al. 2005; Ochi et al. 2009). Nevertheless, the dual-foraging strategy is not consistent among procellariforms, neither among populations of the same species or from year to year within the same population (e.g. Baduini and Hyrenbach 2003). Instead, if resources are abundant, birds may exclusively perform short foraging trips that presumably allow to fulfil both chick's and adults' energetic requirements (e.g. Baduini 2002). Therefore, the dual-foraging strategy is thought to be a facultative response to annual or geographic variation in trophic conditions around breeding sites (e.g. Paiva et al. 2010a,b,c; Ochi et al. 2016).

Understanding the decisional processes by which seabirds determine their levels of nest visiting is essential to comprehend parental behaviour and chick provisioning (Weimerskirch 1999). While some studies suggest that parental effort is regulated by a fixed level of investment (e.g. Ricklefs 1992; Hamer and Hill 1993,1994), others show that birds adjust provisioning in response to the energetic needs of their chicks (e.g. Weimerskirch et al. 1997; Granadeiro et al. 2000; Ochi et al. 2009). New findings also suggest that parents synchronize nest attendances in order to avoid exposing the chick to prolonged periods of starvation (e.g. Congdon et al. 2005; Shoji et al. 2015; Tyson et al. 2017; Wojczulanis-Jakubas et al. 2018). However, the extent to which pair collaborative behaviour has an adaptive value and promotes individual fitness is still speculative and deserves further investigation (Grissot et al. 2019). Therefore, creating a unified approach that integrates the responses of each family member to all the others is essential to comprehend how seabirds regulate parental care. In this perspective, ecological models allow to investigate the processes and interactions among different components of a system, through which hypotheses can be tested and predicted (Jørgensen 1994). In particular, dynamic models account for process-based and time-dependent variations in the state of a target system, enabling a deeper understanding of its components' behavior throughout time (Jørgensen and Bendoricchio 2001). These models are also useful to recreate conditions that are difficult to test and/or control otherwise, and to predict how the system responds and adapts when those conditions are substantially changed (e.g. Bastos et al. 2016a; 2018). Therefore, dynamic models are particularly suitable to complement the limitations of field studies in the manipulation and/or monitoring of key parameters, such as those related to the individuals' energetic requirements and to environmental conditions (e.g. Langton et al. 2014).

Using the Cory's shearwater as a test-species, we developed a dynamic model to explore the parental provisioning dynamics of long-lived seabirds during chick rearing (from egg hatching to fledging of the young), considering physiologic constraints and behavioural decisions of breeding pairs under contrasting environmental scenarios. For this, we tested different hypotheses regarding potential mechanisms implicated in the foraging allocation-decision of breeding Cory's shearwaters, assuming sequential adaptive compromises among the three family members (the focal bird, the chick and the partner). Furthermore, we simulated variations in local foraging conditions through changes in the adults' mass gains during local foraging trips to test whether the optimal solutions to these decisions/adaptive compromises change along a gradient of resources availability around breeding sites. Overall, we aim to address three main questions: (1) how breeding individuals respond to energetic constraints due to both reproductive costs and food availability, (2) how these constraints lead to chick provisioning behaviour and parental coordination, and (3) how the resulting decisions have implications in foraging effort, chick's growth and adults' body condition. We hypothesize that the developed modelling approach can contribute to increase understanding about the mechanisms underlying seabirds' parental behaviour during chick rearing, including the extent to which adaptive compromises among family members are determined by foraging conditions.

3.3 Methods

3.3.1 Model settings

The model was parameterized taking into account data from Cory's shearwaters, although complementary information from other shearwater species was also used in the absence of species-specific data. The time unit used in the model was the hour in order to capture short-term variations in the chick's nutritional status, for a simulation extent of 2300 hours corresponding to the full period of chick rearing for the study species (i.e. 96 day; Granadeiro 1991). We used the STELLA software (version 9.0.3; Systems Thinking for Education and Research; from isee Systems) for the construction of the dynamic model. All details and full explanations on the model implementation, including equations used in the model construction are available in Supporting information (Appendix H and I).

3.3.2 Model structure and functioning

To investigate the parental provisioning dynamics of Cory's shearwaters during chick rearing, four sub-models were designed in order to (Figure 10): (a) recreate potential mechanisms underlying the allocation of foraging effort by breeding birds, considering the adults' body condition, the chick's nutritional status and coordination between breeding pairs; (b) simulate adults' net energy gains, in terms of mass changes, in relation to foraging trip duration; (c) generate meal sizes attributable to the duration of foraging trips; and (d) predict the growth of the chick given the balance between gains from provisioning and physiologic/metabolic losses.

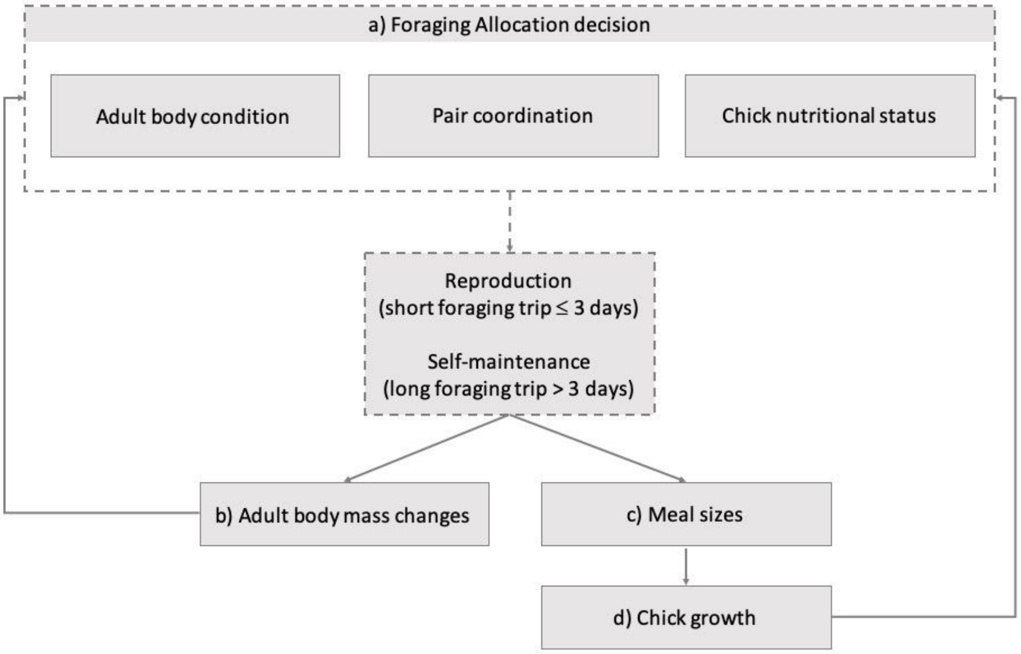


Figure 10 - Conceptual diagram of the dynamic model to predict the parental provisioning dynamics of Cory's shearwaters during chick rearing . The model is composed by different dynamic sub-models and their interactions: (a) potential mechanisms underlying the allocation of foraging effort, in terms of investment in chick provisioning (short foraging trips) or self-feeding (long foraging trips), based on adults' body condition, chick's nutritional status and coordination between breeding pairs; (b) adults' net energy gains (in terms of mass changes) in relation to foraging trip duration, with influence in the body condition of adult birds; (c) meal sizes attributable to the duration of foraging trips, with influence in the chick's growth; and (d) chick's growth given the balance between gains from provisioning and physiologic/metabolic losses, with influence in the chick's nutritional status.

3.3.2.1 Foraging-allocation decisions

The model was prepared to simulate four hypotheses regarding potential mechanisms driving the Cory's shearwaters foraging-allocation decisions (FADs) (Figure 11). The allocation of foraging effort by breeding Cory's shearwaters was integrated in the modelling process in terms of the function of a foraging trip (chick provisioning vs self-feeding), through which birds decide to allocate energy either to invest in chick provision (which triggers a short foraging trip) or to ensure own survival (which triggers a long foraging trip) (Weimerskirch et al. 1994) (Figure 11; Appendix H). Our approach was developed under the conceptual framework of the life-history theory (Stearns 1992) thus breeding birds do not compromise survival at reproductive expenses in all hypotheses considered (Drent and Daan 1980) (Figure 11). In particular, adult birds admit lowering their body condition up to 12% of their average body mass (hereinafter, critical body mass threshold for reproduction; 'Lean body mass' in Figure 11), considering the safety margin of fat reserves retained by a similar species, the Sooty shearwater (*Ardenna grisea*), throughout chick rearing (Weimerskirch 1998). Consequently, if depleted in body reserves birds prioritize self-feeding, engaging in a long foraging trip to build up body reserves independently of the chick's nutritional status (Weimerskirch 1999) (Figure 11). Thereafter, the mechanisms driving the allocation of foraging effort by Cory's shearwaters assume sequential adaptive compromises among family members taking into account the hypotheses considered (Figure 11):

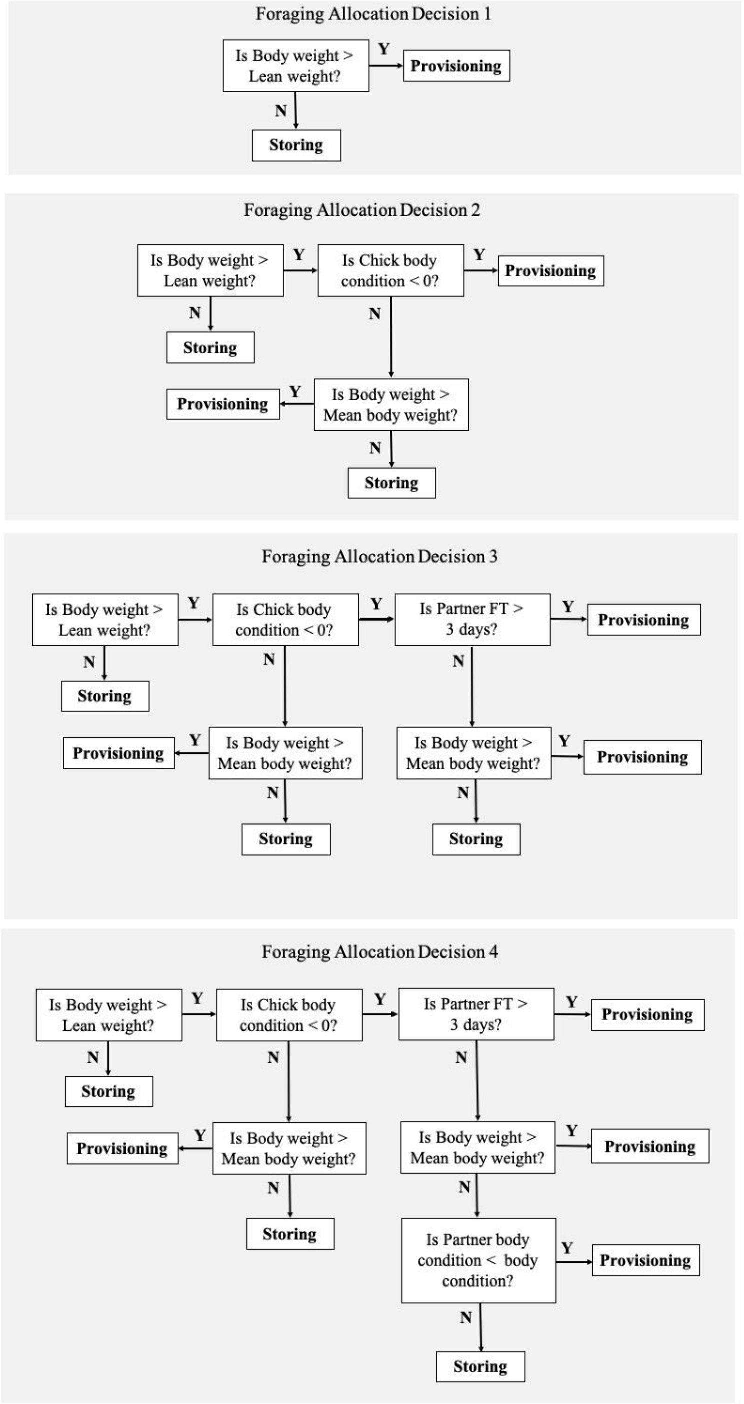


Figure 11 - Conceptual diagram of the Cory's shearwaters foraging-allocation decisions during chick rearing , in terms of chick provisioning (i.e. short foraging trips as ‘Provisioning’) or self-feeding (i.e. long foraging trips as ‘Storing’). Arrows are affirmative (Y = Yes) or negative (N = No). Foraging-allocation decisions (FADs) are sequential and assume adaptive compromises among family members: FAD 1 - provisioning is determined by the adults’ critical body mass threshold for reproduction; FAD 2 - based on FAD 1, provisioning is determined by short-term variations in chick’s nutritional status; FAD 3 - based on FAD 2, provisioning is determined by the partner’s allocation decision; FAD 4 - based on FAD 3, provisioning is determined by the partner’s body condition. Variables description: ‘Body weight’: adult body mass (in grams) at t_x; ‘Mean body weight’: adult body mass (in grams) at t_0; ‘lean weight’: 12% below the adult mean body weight (i.e. critical body mass threshold for reproduction); ‘Chick body condition’: chick nutritional status (index) at t_x; ‘Partner FT’: partner foraging trip duration at t_x: ‘body condition’: adult body condition (index) at t_x; ‘Partner body condition’: partner body condition (index) at t_x. Full explanations on the sub-models implementation (Appendix H) and equations (Supporting Info 2) are available in Supporting information.

FAD 1 – **Chick provisioning is determined by the adults' critical body mass threshold for reproduction:** If the critical body mass threshold for reproduction has not been reached, breeding birds prioritize chick provisioning, otherwise self-feeding is assured (Weimerskirch 1999).

FAD 2 - **Chick provisioning is determined by short-term variations in chick's nutritional status**: Based on FAD1, if the critical body mass threshold for reproduction has not been reached, birds evaluate the nutritional status of their chick (see 'Chick growth and body condition' for details on the chick's nutritional status evaluation). Parents of chicks in poor nutritional condition increase reproductive effort by prioritizing chick provisioning (Erikstad et al. 1998). Whenever the chick is in good nutritional condition, if the adult is in poor body condition self-feeding is assured (see ' Adults at-sea mass gains and foraging trip duration' for details on the adults' body condition evaluation). Otherwise, chick provisioning is prioritized.

FAD 3 – **Chick provisioning is determined in response to the partner's allocation decision:** Based on FAD2, parents of chicks in poor nutritional conditions evaluate the partner's allocation decision (i.e. type of foraging trip). If the partner is engaged in a self-feeding trip, chick provisioning is ensured (e.g. Houston and Davies 1985; Jones et al. 2002); However, if the partner is engaged in chick provisioning, the bird evaluates its own body condition. If in a poor body condition self-feeding is prioritized, otherwise chick provisioning is ensured.

FAD 4 - **Chick provisioning is determined in response to the partner's body condition**: Based on FAD 3, parents of chicks in poor nutritional conditions and whose partner is engaged in chick provisioning, evaluate the partner's body condition (see 'Adults at-sea mass gains and foraging trip duration' for details on the partner's body condition evaluation). If the adult presents a good body condition chick provisioning is ensured. However, if the adult in a poor condition, self-maintenance is prioritized only if its own body condition is poorer than that of its partner (e.g. Jones et al. 2002). Otherwise, chick provisioning is assured.

In terms of model conceptualization and functioning, the allocation decision is updated before birds departing on a foraging trip. After selecting a foraging trip type (chick provisioning or self-feeding), the model randomly generates its respective duration, in days, according to probabilistic curves of real data for short (i.e. ≤ 3 days) and long (i.e. > 3 days) foraging trips (see 'Adults at-sea mass gains and foraging trip duration') (Appendix H). At the beginning of the simulation, both parents are assumed to be in the nest and foraging trips are generated in order to recreate the guarding period (i.e. the period during which one of the parent remains in the nest until the chick attains thermoregulatory ability; Warham 1990). Therefore, during the first 5 days post-hatching (assuming the time window in which more than 50% of the chicks are guarded by one of the parents; Granadeiro 1991; Ramos et al. 2003), the delivery of meals to the chick was restricted to a single parent, and parents favoured provisioning (short trips) in all foraging-allocation decision considered (Appendix H). In the last 15 days of chick rearing , parents of chicks in good nutritional condition prioritize longer journeys (Appendix H) in order to replenish self-reserves for migration, and to trigger the necessary stimulus for young birds to leave the nest (Ramos et al. 2003).

3.3.2.2 Chick growth and body condition

The chick body mass (in grams) was calculated throughout chick rearing considering the balance between gains from provisioning (assuming the total amount of food delivered by both parents), and physiological and metabolic losses (in terms of mass) due to defecation, respiration and digestion (Appendix H) (Walsberg and Carey 2006). Meal sizes were attributable to the duration of foraging trips, based on data from Cory's shearwaters breeding at Selvagem Grande (Granadeiro et al. 1998b). Because the chick spends more energy in digestion and excretion in the first hours after receiving a meal (Hamer and Hill, 1993; Hamer et al. 1999), we account for time-dependent variations in food assimilation efficiency (Appendix H), i.e. the rate of mass loss was greater within the first 4h after the chick has been feed, decreasing afterwards (Hamer et al. 1999). An empirical growth curve of real chicks under optimal conditions (Quillfeldt et al. 2007) was used to evaluate the chick's body condition throughout chick rearing . The chick was considered in a good nutritional condition whenever its body mass was greater than the optimal weight, and in a poor condition whenever under this standard (Appendix H).

3.3.2.3 Adults at-sea mass gains and foraging trip duration

The adults' at-sea net energy gains were modelled in terms of mass changes per foraging trip duration, and were used as proxies for resource availability and foraging success around breeding sites (Shaffer et al. 2003). Due to the lack of specific data for the chick rearing period, variations in the body mass of adults were based on gains at sea in relation to the duration of incubation shifts, obtained from birds breeding at Selvagem Grande (Ramos et al. 2009). The threshold for short foraging trips was therefore established in 3 days because, according to the standard deviation of the adults' mass gains per incubation interval (Appendix J), birds admitted to lose weight up to 3 days foraging at sea, recovering their body condition after that (positive mass increments considering variations around the mean). In order to incorporate stochastic variation in the individuals' foraging efficiency throughout the chick rearing period, the duration of short and long foraging trips was generated randomly. For this, the probabilistic curves of short and long foraging trips were calibrated considering the frequency distribution of foraging trip duration at Selvagem Grande, assuming 5 days as the average duration of long foraging trips (Granadeiro et al. 1998b; Paiva et al. 2010a).

As initial simulations' settings (t=0), males were assumed to weight 946.8 g (Granadeiro 1993), females 836.1 g (Granadeiro 1993) and chicks 69.2 g (Granadeiro 1991). The initial body mass of adult birds was assumed to represent the body mass that individuals intend to maintain, on average, throughout the chick rearing period. Therefore, an adult bird was considered in a good body condition whenever its body mass was greater than its initial value and, in contrast, in a poor condition when its body mass was bellow that reference value (Appendix H). Comparisons of body condition between breeding pairs in FAD 4 were based on an index that is continuously updated throughout chick rearing , which measures the proportion of variation in each parent' body mass in relation to its initial weight (Appendix H). The body mass of adult birds was truncated to a maximum, which is equivalent to the proportion of body mass that birds admit to lose in reproduction (i.e. 12% above their initial value, see 'Foraging-allocation decisions'). Overall, this variation considers the total margin of fat reserves used by Sooty shearwaters throughout chick rearing (Weimerskirch 1998).

3.3.3 Environmental scenarios

In order to investigate the responses of breeding birds to variations in local foraging conditions, we assumed a reduction in the adults' net energy gains during short foraging trips (≤ 3 days foraging trips) (Appendix J). For this, the reference scenario was based on the average adult mass gains during incubation shifts of Cory's shearwaters at Selvagem Grande (hereinafter, reference scenario; see 'Adults at-sea mass gains and foraging trip duration').

Two additional hypothetical scenarios were set, which consider: a sharp decrease in foraging conditions based on the lower limit of the variation around the mean (hereinafter, very poor foraging conditions; Appendix J), and an intermediate decrease given the central value between the lower limit and the average mass gains in the reference scenario (hereinafter, poor foraging conditions; Appendix J). Variations in the adults' body mass during foraging trips longer than 3 days remained stable among the environmental scenarios considered (Appendix J).

3.3.4 Data analyses

To investigate the resulting patterns of different allocation decisions under variable local foraging conditions, we analysed the chick's growth curves, the frequency distribution of foraging trip duration and variations in adults' body mass according to each tested mechanism and environmental scenario considered (see 'Foraging-allocation decision' and 'Environmental scenarios'). The frequency distribution of foraging trip duration and variations in adults' body mass were described assuming breeding females for demonstrative purposes. Since the model simulations assume stochasticity in the generation of foraging trip duration, the mean and standard deviation of 100 independent simulations (i.e. 100 breeding pairs) were considered in the results for the entire chick rearing period.

A Kruskal-Wallis was also used to understand whether females' body mass, chick feeding frequencies (in terms of nest visits by at least one parent) and chick growth rates diverged among foraging-allocation decisions for each environmental scenario (assuming 100 independent simulations/breeding pairs for each foraging-allocation decision and environmental scenario considered). For each simulation, we considered: (1) the average female' body mass during chick rearing , expressed in terms of body condition, i.e. variation of body mass in relation to their initial value (proportion); (2) the proportion of nights when food was received by the chick during chick rearing , expressed as chick feeding frequency; and (3) the average daily changes in chick mass during chick rearing , expressed as chick growth rate (grams per day). These analyses considered only the period between the post-guard and the end of mid-chick rearing (chicks between 5 and 55 days of age), in order to limit the uncertainty effect of the chicks thermoregulatory independence and emancipation from the nest before fledgling (for which particular dynamics should be addressed under specific frameworks; e.g. Varpe et al. 2004; Catry et al. 2009). The Kruskal-Wallis Test was performed using the ´kruskal.test´ function in the R package ´stats´ (R Development Core

Team 2018), and all pairwise *post-hoc* multiple comparisons were analysed using a Dunn's test, applying the ´DunnTest´ function (argument "method = Holm") in the R package ´DescTools´ (R Development Core Team 2018). All data plots were generated in 'ggplot2' (R Development Core Team 2018).

3.4 Results

3.4.1 Patterns of chick provisioning behaviour and foraging effort along a gradient of local foraging conditions

3.4.1.1 Chick growth

For all FADs and scenarios considered, chick growth curves were compared with the reference growth of chicks under optimal breeding conditions (hereinafter, optimal growth curve) (Quillfeldt et al. 2007). Under such circumstances, chicks presented a rapid linear increase in body mass during the first 30 days after hatching, followed by a decrease in growth rate, reaching the asymptotic mass at around 1100 g (Figure 12). During the last month of chick rearing , chicks tended to lose weight, attaining masses at fledgling of nearly 850 g (Figure 12).

According to our simulation results, in all FADs, chicks tended to approximate the optimal growth curve as foraging conditions improved around the breeding colony (Figure 12). Despite a slight underestimation of asymptotic and fledgling masses, the body mass of chicks in the reference scenario peaked between 950 g (FAD 1, FAD 3 and FAD 4) and 1000 g (FAD 2), and chicks fledged with nearly 800 g in all FADs considered (Figure 12). Under poorer foraging conditions, chicks presented slower growth rates and relative lower masses at fledgling according to all FADs (around 725 g in the scenario of poor foraging conditions), which was particularly marked in the scenario of very poor foraging conditions (body mass of chicks nearly 620 g at fledgling) (Figure 12).

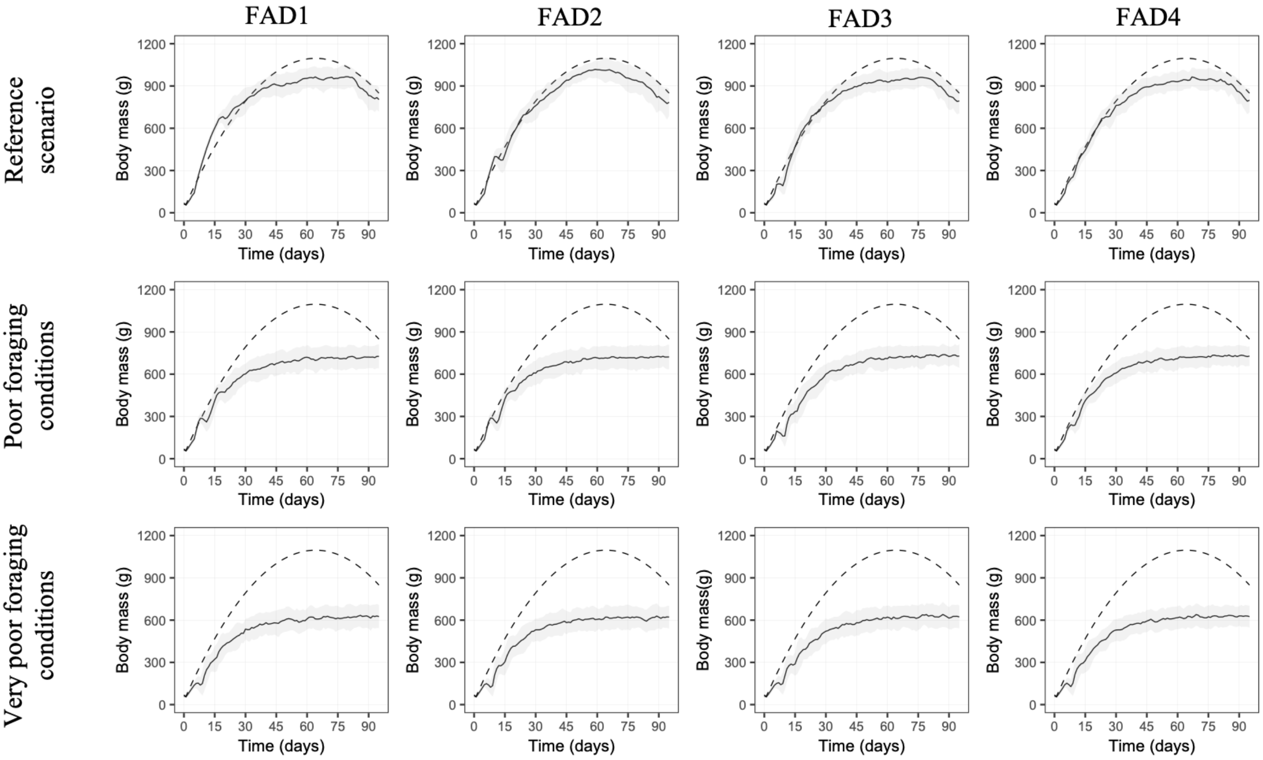


Figure 12 - Average chick's growth curves simulated throughout chick rearing (solid lines), according to different foraging-allocation decisions (vertical reading) and environmental scenarios (horizontal reading). Foraging-allocation decisions (FADs) assume sequential adaptive compromises among family members: FAD 1 - provisioning is determined by the adults' critical body mass threshold for reproduction; FAD 2 - based on FAD 1, provisioning is determined by short-term variations in chick's nutritional status; FAD 3 - based on FAD 2, provisioning is determined by the partner's allocation decision; FAD 4 - based on FAD 3, provisioning is determined by the partner's body condition. Body mass is presented as mean ± standard deviation (n=100 independent simulations). The dashed line presents the reference empirical growth of real Cory's shearwater chicks under optimal breeding conditions (Quillfeldt et al. 2007).

3.4.1.2 Frequency distribution of foraging trip duration

In all FADs, the frequency of short trips ($\leq$ 3 days) tended to increase as foraging conditions improved around the breeding colony (Figure 13). In particular, breeding birds tended to perform around 90% of short trips in the reference scenario (circa 10% of long trips), 80% in the scenario of poor foraging conditions (circa 20% of long trips), and 70% in the scenario of very poor foraging conditions (circa 30% of long trips) (Figure 13).

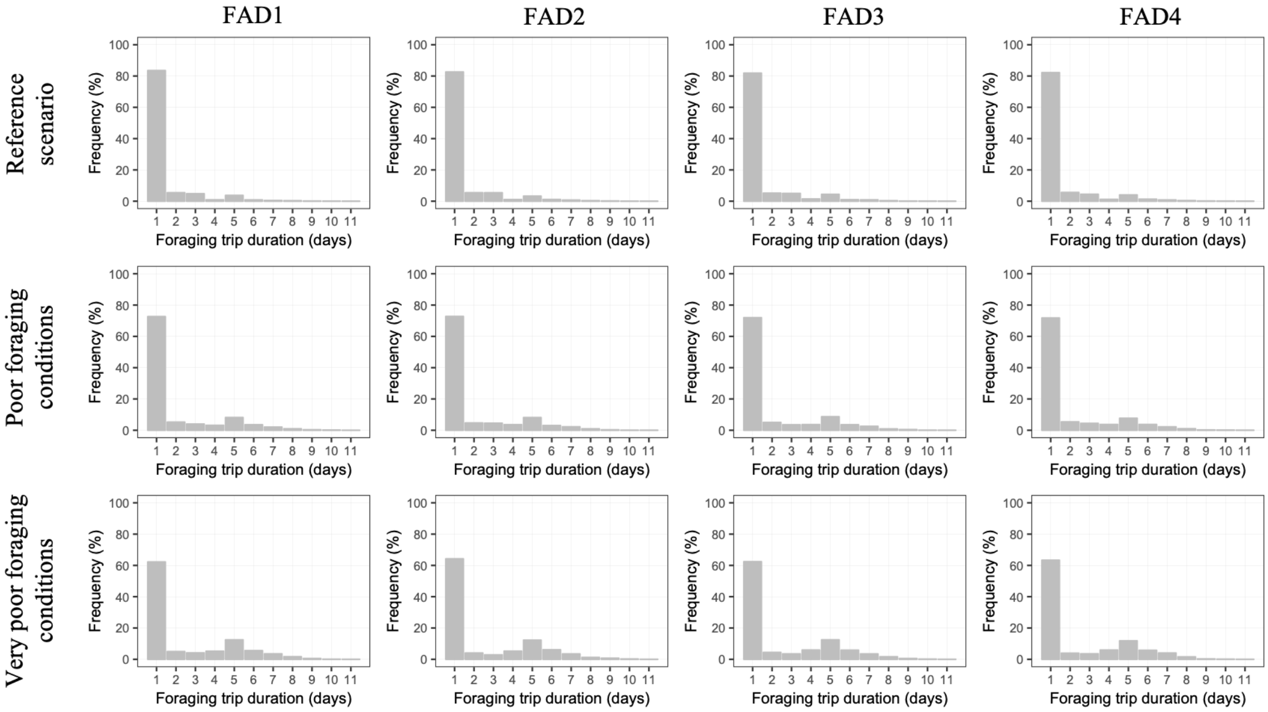


Figure 13 - Frequency distribution of the duration of females' foraging trips simulated throughout chick rearing , according to different foraging-allocation decisions (vertical reading) and environmental scenarios (horizontal reading). Foraging-allocation decisions (FADs) assume sequential adaptive compromises among family members: FAD 1 - provisioning is determined by the adults' critical body mass threshold for reproduction; FAD 2 - based on FAD 1, provisioning is determined by short-term variations in chick's nutritional status; FAD 3 - based on FAD 2, provisioning is determined by the partner's allocation decision; FAD 4 - based on FAD 3, provisioning is determined by the partner's body condition. The frequency distribution of foraging trips duration represents cumulative results from 100 independent simulations.

3.4.1.3 Adults' body mass

In all FADs and scenarios considered, females lost mass during the post-hatching stage, recovering thereafter to levels that tended to remain relatively stable throughout chick rearing (Figure 14), with exception of FAD 2 in the reference scenario. In particular, according to FAD 1, females kept their body mass on average at 800 g throughout chick rearing, regardless of variations in foraging conditions around the breeding colony (Figure 14). In the final stage of the chick rearing period in the reference scenario, females presented a clear increase in body mass to nearly 920 g (Figure 14).

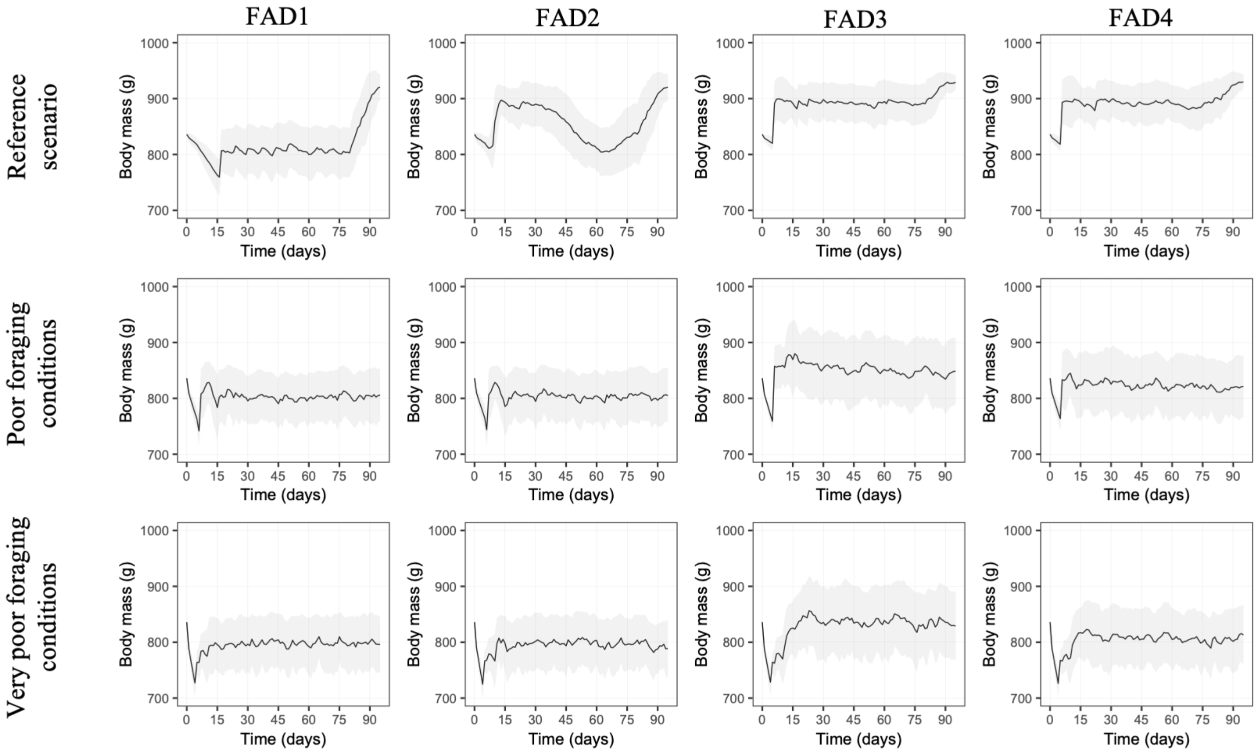


Figure 14 - Variation in females' average body mass throughout chick rearing , according to different foraging-allocation decisions (vertical reading) and environmental scenarios (horizontal reading). Foraging-allocation decisions (FADs) assume sequential adaptive compromises among family members: FAD 1 - provisioning is determined by the adults' critical body mass threshold for reproduction; FAD 2 - based on FAD 1, provisioning is determined by short-term variations in chick's nutritional status; FAD 3 - based on FAD 2, provisioning is determined by the partner's allocation decision; FAD 4 - based on FAD 3, provisioning is determined by the partner's body condition. Body mass is presented as mean ± standard deviation (n=100 independent simulations).

Likewise, in FAD 2, females maintained their body mass at around 800 g throughout chick rearing in both scenarios of poor and very poor foraging conditions (Figure 14). In the reference scenario, they presented a marked fluctuation in average weight along chick rearing , increasing body mass up to 900 g at the beginning of the brooding period, gradually decreasing to 800 g by the end of mid-chick rearing (Figure 14). Females tended to regain mass during the last month of chick rearing , reaching on average 920 g by the end of the breeding season (Figure 14). According to FAD 3 and FAD 4, females maintained their body mass at around 900 g throughout chick rearing in the reference scenario, presenting a slight increase to 930 g in the last stage of chick rearing (Figure 14). In the scenario of poor foraging conditions, both FADs promoted a slight decrease in females body mass throughout chick rearing (Figure 14). By the end of chick rearing , females presented body masses on average above 850 g in FAD 3, and under 850 g in FAD 4 (Figure 14). In the scenario of very poor conditions, although with a less pronounced trend in the reduction of body masses along chick rearing , the body mass of females approximated 850 g in FAD 3, while in FAD 4 tended on average to 800 g (Figure 14).

3.4.2 Comparisons among foraging-allocation decisions

Our results indicate significant differences in females' body condition among all but FAD 3 and FAD 4 in the reference scenario ($\chi^2 = 297.2$, df = 3, $P < 0.001$) (Figure 15).

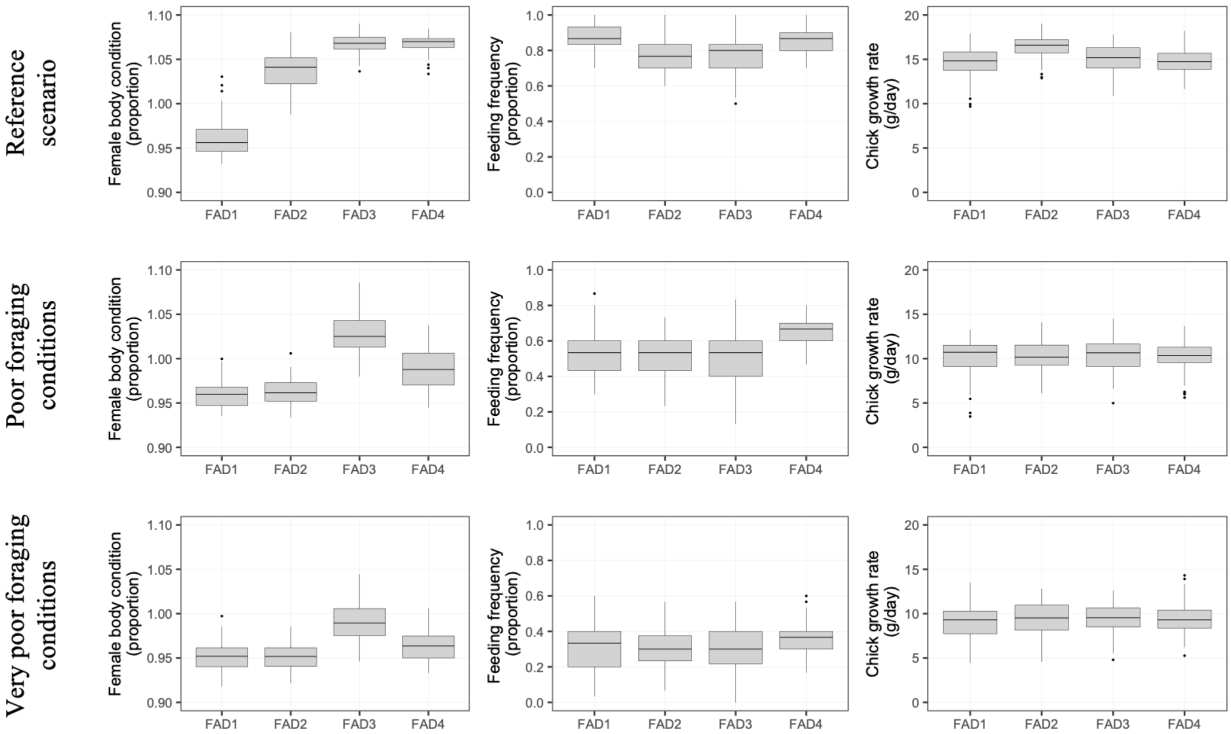


Figure 15 - Variation in females' body condition, feeding frequency and chick growth rate (vertical reading) according to different foraging-allocation decisions and environmental scenarios (horizontal reading) for the period between the post-guard and the end of mid-chick rearing (chicks between 5 and 55 days of age). Foraging-allocation decisions (FADs) assume sequential adaptive compromises among family members: FAD 1 - provisioning is determined by the adults' critical body mass threshold for reproduction; FAD 2 - based on FAD 1, provisioning is determined by short-term variations in chick's nutritional status; FAD 3 - based on FAD 2, provisioning is determined by the partner's allocation decision; FAD 4 - based on FAD 3, provisioning is determined by the partner's body condition. The lower and upper limits of each box represent the first and third quartiles, respectively, and the line inside each box represents the median (n=100 independent simulations). The bottom and top limits of vertical lines represent the minimum and maximum values, respectively. Dots outside the first and third quartiles range are plotted as outliers.

In particular, FAD 2 allowed females to significantly increase body condition in relation to FAD 1, while FAD 3 and FAD 4 were the most profitable decisions when compared to FAD 1 and FAD 2 (Figure 15). Overall, females lost 4% of their initial body mass according to FAD 1, gaining 4% in FAD 2, and 7% in both FAD 3 and FAD 4 (Figure

15). Concerning the proportion of nights when food was received by the chicks, breeding parents using FAD 1 and FAD 4 provisioned their chicks at significantly higher feeding frequencies when compared to FAD 2 and 3 ($\chi^2 = 88.3$, df = 3, $P < 0.001$), i.e. in 87% of the nights according to FAD 1 and FAD 4, and in 77% and 80% of the nights in FAD 2 and FAD 3, respectively (Figure 15). The chicks grew at significantly greater rates in FAD 2 ($\chi^2 = 72.7$, df = 3, $P < 0.001$), presenting daily increments of 17 g/day, in contrast to 15 g/day in FAD 1, FAD 3 and FAD 4 (Figure 15).

In the scenario of poor foraging conditions, significant differences in females' body condition were found among all but FAD 1 and FAD 2 ($\chi^2 = 259.2$, df = 3, $P < 0.001$). FAD 3 and FAD 4 promoted significant increments in the females' body condition in relation to FAD 1 and FAD 2, although FAD 3 yielded higher gains when compared to FAD 4 (Figure 15). In terms of the frequency of food delivered at the nest, FAD 4 significantly increased the regularity of provisioning in relation to FAD 1, FAD 2 and FAD 3 ($\chi^2 = 95.9$, df = 3, $P < 0.001$) (Figure 15). Overall, according to FAD 1 and FAD 2, females lost 4% of their initial weight, while in FAD 4 they reduced 1% of their initial body mass and in FAD 3 they increased body condition in 3% (Figure 15). In terms of provisioning frequency, chicks received meals in 53% of the nights according to FAD 1, FAD 2 and FAD 3, and were attended by at least one parent in 67% of the nights in FAD 4 (Figure 15). No significant differences were found in the growth of chicks among FADs ($\chi^2 = 0.7$, df = 3, $P = 0.8$), which presented mass increments ranging between 10 and 11 g/day (Figure 15).

Under a sharp environmental decrease in the scenario of very poor foraging conditions, the results indicate significant differences in females' body condition among all but FAD 1 and FAD 2 ($\chi^2 = 162.8$, df = 3, $P < 0.001$) (Figure 15). Like in the scenario of poor foraging conditions, both FAD 3 and FAD 4 promoted significant increments in the body condition of females when compared to FAD 1 and FAD 2 (Figure 15), although FAD 3 contributed to greater gains than FAD 4 (Figure 15). Females lost 5% of their initial body mass according to FAD 1 and FAD 2, 4% according to FAD 4 and 1% in FAD3 (Figure 15). FAD 4 promoted more regular feeding intervals than all other FADs in the scenario of very poor foraging conditions ($\chi^2 = 15.6$, df = 3, $P < 0.01$), allowing breeding birds to increase feeding frequency from nearly 30% of the nights according to FAD 1, FAD 2 and FAD 3, up to 37% of the nights according to FAD 4 (Figure 15). All FADs promoted similar chick' mass gains in this scenario ($\chi^2 = 2.3$, df = 3, $P = 0.5$), which ranged between 9 and 10 g/day (Figure 15).

A full description of all parameters that varied significantly among FADs in terms of females' body condition, chick's feeding frequency and chick's daily growth rate are shown in Appendix K.

3.5 Discussion

The interpretation and discussion of the results follow a two-fold assessment. We firstly analysed whether the allocation decisions tested were able to reproduce realistic patterns of Cory's shearwaters provisioning behaviour along a gradient of local resources availability. Since the model was parameterized with data coming from individuals breeding at Selvagem Grande (Selvagens sub-archipelago of Madeira), simulation outputs were interpreted using this colony as the reference for comparisons. After inspecting the performance of the simulated patterns, we explored the role of parents' body condition in chick provisioning behaviour, the implications of different pair collaborative strategies in individual fitness, and how birds might adapt these responses to local resources availability.

3.5.1 Comparisons between simulated and empirical patterns

In the chick rearing seasons of 1991, 1993 and 1994 at Selvagem Grande, chicks (between 20 and 50 days of age) received meals in 77% of the nights (mean of the 3 years), attaining nearly 900 g in the end of the study period (Hamer and Hill 1993; Hamer et al. 1999). However, in 1997, chicks were 30% lighter (e.g. 22 August 1997: 519.9±122.6 g, Granadeiro et al. 1998b; 19 August 1993: 673.8±87.2 g, Hamer and Hill 1994), which was attributable to a reduction of nearly 34% in the nights when chicks were fed by at least one of the parents (chicks fed in only 52% of the nights in 1997; Granadeiro et al. 1998b). Our simulation results seemed to capture realistic variations in the Cory's shearwaters' breeding effort between years of contrasting environmental conditions around Selvagem Grande. In particular, the growth of chicks in the reference scenario was the closest to field observations in Selvagem Grande in 1991, 1993 and 1994 (i.e. chicks' body mass 50 days after hatching: FAD1: 918±84 g; FAD2: 977±59 g; FAD 3: 918±74 g: FAD 4: 908±65 g), while the simulated patterns approximated those obtained in 1997 as the adults' energy gains were reduced during local foraging trips. In particular, the mean body mass of chicks was predicted to decrease between 23% and 29% in the scenario of poor foraging conditions (i.e. 50 days post-hatching: FAD1: 685±68 g; FAD2: 691±75 g; FAD3: 704±73 g; FAD4: 699±80 g), and between 34% and 38% in the scenario of very poor foraging conditions (i.e. 50 days post-hatching: FAD1: 607±89 g; FAD2: 603±88 g; FAD3: 603±85 g; FAD4: 588±76 g), while feeding frequencies declined between 14% and 25% in the scenario of poor foraging conditions (i.e. feeding frequency of chicks between 25 and 55 days of age: FAD1: 73%; FAD2: 70%; FAD3: 77%; FAD4: 80%), and between 28% and 35% in the scenario of very poor foraging conditions (i.e. feeding frequency of chicks between 25 and 55 days of age: FAD1: 60%; FAD2: 60%; FAD3: 63%; FAD4: 67%).

These results suggest that the adults' mass gains used to parameterize the model in the reference scenario (recorded in the breeding season of 2006) were able to capture, within realistic limits, the foraging ability of Cory's shearwaters breeding at Selvagem Grande in years of presumably standard foraging conditions. In fact, the body mass of real chicks 60 days after hatching (1012±113 g; Catry et al. 2009) combined with a relatively high fledging success (88% fledging per egg hatched; Alonso et al. 2009) suggest favourable breeding conditions in 2006. Furthermore, despite the lack of data on the foraging effort of breeding birds on Selvagem Grande in 2006, the duration of foraging trips in subsequent years (i.e. 2.1±3.7 days in 2007 and 2.4±4.3 days in 2008; Paiva et al. 2010a) indicates that individuals tend to maintain high frequency of short trips between reproductive seasons in this colony. Conversely, in 1997, birds spent more time at sea (i.e. males: 3.3±2.3 days and females 3.0±2.0 days; Granadeiro et al. 1998b), supporting the idea that local foraging conditions were comparatively poorer in this breeding season. Likewise, according to our simulation results, individuals remained less time away from the colony in the reference scenario (i.e. chicks between 25 and 55 days of age: FAD1: 1.4 ± 1.2 days; FAD2: 1.3 ± 1.0 days, FAD3: 1.4 ± 1.1 days, FAD4: 1.4 ± 1.2 days), increasing the duration of foraging trips in the scenario of poor foraging conditions (chicks between 25 and 55 days of age: FAD1: 2.0 ± 1.9 days; FAD2: 2.0 ± 1.8 days, FAD3: 2.1 ± 1.9 days, FAD4: 2.1 ± 1.9 days) and very poor foraging conditions (chicks between 25 and 55 days of age: FAD1: 2.5 ± 2.1 days; FAD2: 2.5 ± 2.1 days, FAD3: 2.5 ± 2.2 days, FAD4: 2.5 ± 2.2 days).

Our results support the idea that, in 1997, the observed reduction in chick feeding frequencies was probably triggered by a decrease in the foraging efficiency of adults during short foraging trips, as a consequence of food shortage around Selvagem Grande in this specific year (Granadeiro et al. 1998b). The authors also hypothesized that in years of normal abundance of resources birds could not following the dual-foraging strategy (Granadeiro et al. 1998b). However, the recent frequent tracking of Cory's shearwater from Selvagem Grande show that during chick rearing birds always show patterns of a dual-foraging strategy (Paiva et al. 2010a,b,c). In our predictions, birds were using the dual-foraging strategy in the reference scenario (e.g. birds had negative intakes during short foraging trips), and yet were able to obtain realistic patterns of chick growth in years of presumably normal foraging conditions around Selvagem Grande. It is certainly important to highlight that the adults' net energy gains used to parameterize the model in the reference scenario were recorded during the incubation period, thus possibly deviating from those in the chick rearing of the same year. Alternatively, conditions may have not changed abruptly between these two periods and the dual-foraging may be generally used by Cory's shearwaters at Selvagem Grande, to compensate for low or unpredictable resource levels close to the breeding colony among breeding seasons. In fact, other studies suggest that the ocean area surrounding the Selvagem Grande is characterized by low marine productivity (Ramos et al. 2003; Catry et al. 2009; Paiva et al. 2010a,b,c), forcing Cory's shearwaters to undertake longer foraging trips towards the profitable upwelling system of the NW African coast (Mougin et al. 1997; Catry et al. 2009). Notably, birds from Selvagem Grande reach the African coast within 1.5 days (Mougin et al. 1997), what is in line with the average positive mass increments recorded in incubation shifts lasting more than 3 days during 2006. Regardless of whether the dual-foraging strategy is optional for breeding shearwaters in Selvagem Grande, the degree of investment in short trips by breeding birds is certainly linked to the marine productivity around this colony among breeding seasons (Granadeiro et al. 1998b).

3.5.2 Implications of state-dependent parental care in provisioning behaviour

A key parameter when studying provisioning behaviour is the body condition of adults. According to the life-history theory, breeding birds do not admit lowering their body mass beyond the threshold at which future reproduction is compromised (Stearns 1992). Thus, foraging-allocation decisions are highly dependent on the amount of body reserves that adult birds retain during the breeding season (Chastel et al. 1995). Since previous studies examining the Cory's shearwater provisioning behaviour at Selvagem Grande did not assess the body condition of breeding birds, direct comparisons with our results cannot be made. However, empirical studies in procellariforms show that breeding adults feed their chicks at higher rates when they are heavier, reducing provisioning as a consequence of a decrease in mass reserves (e.g. Tveraa et al. 1998; Weimerskirch et al. 2000; Ochi et al. 2016). This suggests that both the levels of chick provisioning and self-feeding are affected by the availability of resources encountered in the colony surroundings.

According to our simulation results, when parental effort was regulated by a fixed level of investment, the body condition of breeding individuals did not change due to variations in local trophic conditions (i.e. FAD1: very poor: 0.95; poor: 0.96; reference: 0.96). On the other hand, birds that adjusted provisioning in response to the chicks' needs increased body reserves as more resources were available in the colony surroundings (i.e. FAD 2: very poor: 0.95; poor: 0.96; reference: 1.04); which is in line with several empirical studies on procellariforms (e.g. Weimerskirch et al. 2000; Ochi et al. 2016); including for Cory's shearwaters breeding at Berlengas and Porto Santo (Madeira archipelago) (Paiva et al. 2017; Avalos et al. 2017). In fact, breeding individuals responding to short-term variations in the chicks' energetic requirements (FAD 2) were able to significantly increase body condition when compared with birds unwilling to do so (FAD1) in the reference scenario. These results indicate that a compensatory response to the chick needs (FAD2) allowed breeding birds to improve self-feeding under better foraging conditions, thus accumulating additional body reserves during chick rearing (Ochi et al. 2016). Notably, chicks received meals in a significant less proportion of nights and yet presented higher average daily growth rates. This suggests that, despite being feed at submaximal rates, chicks were assimilating food more easily thus growing and developing faster (Schaffner 1990; Hamer et al. 1999). Besides, by adjusting provisioning to the chick's needs (FAD2), parents avoided over-feeding their nestlings as observed in new-born birds of parents using a fixed level of provisioning effort during the first month of chick rearing in the reference scenario (i.e. FAD1 in Figure 12). Conversely, under poorer foraging conditions, birds presented similar body condition and chicks' feeding frequency of individuals without this regulatory capability (FAD 1), indicating that parents were having difficulties in regulating provisioning according to the chick needs. Therefore, when local resources are limited, an ideal strategy is likely to be feeding the chick as often as possible, continuously allocating body reserves in order to maximize provision rates (Weimerskirch 1998, 1999).

3.5.3 The role of parental cooperation in individual fitness

A behavioural response thought to have major implications in chicks provisioning is the coordination of parental effort between breeding partners. For parents using a dual-foraging strategy, the coincidence of long foraging trips may represent extended periods of waiting for food by the chick, thus resulting in a periodic risk of starvation and consequently chick growth retardation (e.g. Schaffner 1990). In order to mitigate such mismatch, we assumed that breeding individuals synchronize their foraging activities in a way that by the time one parent is in a long trip, the other ensures chick provisioning; i.e. the partner should compensate in order for the offspring to survive (Houston and Davies 1985; Jones et al. 2002). Furthermore, we also considered that, if coordination allows the pair to increase provisioning efficiency (Congdon et al. 2005; Tyson et al. 2017), it should be higher when pairs are forced to work harder (chicks in poor condition) than when their workload is lightened (chicks in good condition) (e.g. Mariette and Griffith 2015). In this perspective, each parent adjusts its own effort in response to that of its partner so that, whenever the chick is in a poor body condition (bellow the optimal growth rate), one compensates for a reduction in the partner' provision effort (during self-feeding long trips), thus maximizing provisioning rates (e.g. Bijleveld and Mullers 2009). Nevertheless, when both parents are disposed to invest in provisioning, the pair becomes more flexible in their choice of possible strategies and a conflict over bi-parental care can arise (Jones et al. 2002), i.e. the amount of care that one of the parents is willing to provide given the partner's effort. To resolve such conflict, we conceptualized two possible strategies of parental cooperative behaviour: birds that try to minimize the cost of parental care solely for themselves (hereinafter, partial cooperative behaviour; FAD 3), and birds that try to minimize the cost of parental care for the pair as a whole (hereinafter, full cooperative behaviour; FAD 4).

According to our results, the degree of cooperation between partners had different implications in the adults' body condition and chicks feeding frequency. In particular, when compared with birds lacking this regulatory response (FAD 2, hereinafter uncooperative birds), both strategies were effective in maintaining adults in a better body condition regardless of variations in local foraging conditions. Nevertheless, only fully cooperative birds were able to significantly increase the frequency of food delivers at nest while simultaneously promoting increments in the adults' body condition. In fact, while in FAD 3 parents shift most of the care to the partner in order to allocate more resources to self-feeding, in FAD 4 coordination is determined by which partner is in a greater need of a long self-maintenance foraging trip. Therefore, partially cooperative individuals increased body condition by limiting their investments in reproduction to the minimum, thus not being able to increase the frequency of chick provisioning in relation to uncooperative pairs. This denotes a failure in coordination between parents according to this strategy.

From another perspective, fully cooperative birds delivered significantly more regular meals to the chicks and, simultaneously, increased body condition in comparison with uncooperative birds in all environmental scenarios considered. Curiously, this strategy was not beneficial to the nestlings in terms of growth rate, probably because coordination results in a lower amount of food to the chicks as, occasionally, only one parent allocates energy to provisioning (less food is brought to the nest at once). Therefore, this trend becomes more evident under good foraging conditions because uncooperative pairs end up delivering double meals more frequently, leading to a significant increase in the daily chick growth rates in relation to fully cooperative birds in the reference scenario. On the other hand, in terms of the number of nights when chicks were unfed, pair collaborative behaviour supported more efficient levels of parental investment, which may be crucial to decrease the likelihood of chicks' starvation particularly under poorer environmental circumstances. In fact, these results are in agreement with empirical studies, which found that a higher level of coordination is associated with lower variability in the duration of inter-feeding intervals, although this apparently did not affect chick growth (Wojczulanis-Jakubas et al. 2017; Grissot et al. 2019). Besides, by sharing the cost of parental investment, each member of the pair may economize body reserves throughout chick rearing , which is perhaps indicative of a greater fitness of the whole family. Interestingly, according to our predictions, the range of variation in the body condition of fully cooperative birds between years of contrasting foraging conditions was of 11% (-4% in years of very poor foraging conditions and +7 % in the reference scenario), very close to field observations of Yellow-nosed albatrosses (*Diomedea chlororhynchos*) under different breeding conditions (-4% in years of poor breeding conditions and +8 % in years of good breeding conditions, using as reference the body mass of breeding birds in standard breeding conditions) (Weimerskirch et al. 2000).

Overall, our simulation results support the idea that cooperation between partners can be simultaneously used to ensure regular chick provisioning throughout chick rearing , while minimizing the cost of parental investment for the pair as a whole (Roughgarden 2012). It is however important to note that the effectiveness of pair collaborative behaviour tended to decrease as foraging conditions declined in the colony surroundings (smaller differences in adults' body condition and chick feeding frequency between fully cooperative individuals and uncooperative birds). Therefore, under severe scarcity of resources, parents are likely to face the challenge of self-maintenance in a way that impairs their ability to regulate provision according to each other effort, causing coordination to fail (Grissot et al. 2019). Unfortunately, for Cory's shearwaters, the lack of empirical knowledge about the compensatory behaviour between breeding members precludes us to speculate about these predictions. Nevertheless, as a procellariform, its extreme life history characteristics make this species a plausible candidate to which cooperative provisioning is potentially advantageous and, therefore, a likely mechanism underlying its reproductive behaviour.

3.5.4 Evaluation of model assumptions and simulations design

The aim of this study was to test potential mechanisms underlying the parental behaviour of long-lived seabirds along a gradient of local resources availability around breeding sites. For this, we considered the average reproductive pair as the appropriated structural unit to analyse the dynamics among family members during chick rearing . Furthermore, variations in the foraging efficiency of individuals (per environmental scenario considered) were assumed in model predictions by considering stochastic generation of foraging trip duration, according to probabilities of the phenomenon under study. However, in order to compare the responses of breeding individuals among different scenarios of local resources availability, we stabilized the uncertainty effect associated with environmental stochasticity at the foraging trip level (i.e. we did not consider variability in adult's net energy intakes and chick meal sizes per foraging trip duration within each scenario). In this perspective, we built our environmental scenarios under the assumption that the frequency distribution of foraging trip duration is more sensitive to changes in foraging conditions than variations in chicks meal sizes (which not varied among scenarios) (Bolton 1995; Granadeiro et al. 2000; Weimerskirch et al. 2008). Nevertheless, to investigate the parental provisioning dynamics within particular breeding seasons and foraging contexts, it would be important to include variability in the individuals' foraging efficiency both in terms of adults' net energy intakes and meal sizes per foraging trip duration (i.e. individual-level mechanisms underlying provisioning behaviour). In this sense, more detailed processes associated with the regulation of meal sizes according to the chicks' energetic needs, including sex-specific differences in foraging and parental effort (e.g. Paiva et al. 2017), could improve predictions accuracy and mechanistic understanding of parental behaviour. For instance, according to our results, feeding rates in the reference scenario tended to overestimate real data from Selvagem Grande, in part because in real contexts chicks are occasionally attended by parents but not fed (Hamer et al. 1999). When investigating parental behaviour is also important to assess the quality and quantity of information that mates have about each other (Johnstone and Hinde 2006, Hinde and Kilner 2007). In our model, we assumed that each parent has complete information about the other's proximity to the breeding colony (i.e. if the partner is in a short or long foraging trip); and that when both parents regularly attend the nest (i.e. during short trips), they have full knowledge of each other body condition. In this aspect, including processes associated with the transference of information between individuals could be valuable to test the effectiveness of pair collaborative behaviour under more realistic contexts. Finally, the feasibility of comparing simulations with reality was compromised in this study due to the lack of some key parameters from the field (e.g. Cory's shearwaters body condition). In this sense, our approach is a useful to guide strategic data collection to validate models and improve understanding about behavioural processes (e.g. pair collaborative behaviour), while also providing a starting point for the integration of more detailed components with potential of application to other species and environmental contexts.

Chapter 4

Localized control of opportunistic, overabundant species in protected areas: a retrospective modelling approach encompassing future scenarios

Photograph by Andrés de la Cruz 2019

4.1 Abstract

The yellow-legged gull is an opportunistic seabird species, whose worldwide demographic increase in the second half of the 20th century was associated to anthropogenic activities, such as the proliferation of open-air dumps in urban coastal areas. In the small Berlengas archipelago (Peniche, Portugal), the species breeding population reached about 44 000 individuals in 1994, representing a severe ecological pressure in this Biosphere Reserve. In an attempt to control this overpopulation, management actions were implemented in the area, namely, the culling of breeding adults and later egg destruction campaigns. Although the population has been decreasing in recent years, it is unknown how much of this reduction is due to management actions since the closure of open-air dumps in Portugal might also have influenced the yellow-legged gull population trends. We developed a dynamic model to test pertinent explanatory hypotheses for this problem, taking into account retrospective population trends under alternative contexts of food availability and management actions. The model was also used to predict population growth patterns under future management scenarios. Our results show that, despite contributing to reduce birds local abundance, egg destruction alone would not be able to trigger the population decrease observed in the last two decades. Instead, the permanent closure of open-air dumps in 2001 was likely the major driver for the species local decline. In the current context of restricted anthropogenic food sources, our study also suggests that the tendency of the population is to naturally decline. Thus, continuing fertility control campaigns can compromise the future viability of the yellow-legged gull population on the Berlengas Natural Reserve. Our study highlights the interplay between model-based research and ecological monitoring to test the effectiveness of ongoing management programmes and to anticipate the ecological consequences of future control of native species.

Keywords: animal management; culling; fertility control; *Larus michahellis*; open-air dump; population dynamics; yellow-legged gull.

4.2 Introduction

It is currently recognized that wildlife management needs to cope with increasingly complex interactions between wildlife populations, the environment and human activities (Apollonio et al. 2017). In this respect, one of the great challenges in ecological integrity studies is to predict how anthropogenic and environmental changes affect the ecology of species and the composition of biotic communities (Kareiva et al. 1992; Andreasen et al. 2001). Ecological studies have been improved by creating dynamic models that simultaneously attempt to capture the structure and the composition of systems affected by long-term disturbances (Jørgensen 1994, 2001). When properly developed, tested and applied (with insight and with respect to their underlying assumptions), such models are capable of simulating conditions that would be difficult or impossible to understand otherwise (Jørgensen 2001). Therefore, these kinds of models are useful tools to predict how animal populations respond to changes driven by anthropogenic pressures and to investigate the underlying mechanisms responsible for such responses (e.g. Faust et al. 2004). Ecological models are also helpful in supporting technical and administrative decisions by anticipating and prioritizing management efforts directed to specific conservation goals (e.g. Dolbeer 1998).

In the second half of the 20th century, several gull populations (genus Larus) exhibited a tremendous worldwide demographic increase (e.g. Harris 1970; Arizaga et al. 2009; Telailia et al. 2015), triggering disruption in the structure and function of ecosystems through competitive, predatory and pathogenic interactions (Garrot et al. 1993). In an attempt to deal with this problem, gull management programmes have been implemented since the 1970s (e.g. Alvarez 1992; Wanless et al. 1996; Bosch et al. 2002). As common applied measures, they include lethal control by culling of breeding adults, and fertility control either by egg destruction, egg-oiling, substitution of eggs with fake ones, egg shaking and/or egg puncture (Serra et al. 2016). While culling can drastically reduce the density of individuals in the short term (Thomas 1972; Oro and Martínez-Abraín 2007), fertility control has implications on breeding success and, consequently, in the growth rate of populations (Wanless et al. 1996; Serra et al. 2016). Therefore, fertility control entails longer periods to become effective since it has implicit a time lag between its execution and the necessary period for gulls to reach sexual maturity (Thomas 1972). In both cases, management campaigns require intense labour work and involve high financial costs (Serra et al. 2016). Paradoxically, over the last two decades, large gull populations have declined following improved waste management practices, shifting the management paradigm (Mitchell et al. 2004). In fact, the past exponential growth of gulls has been associated with the concomitant increase and intensification of human activities, specifically the proliferation of open-air dumps in urban coastal areas and the development of industrial fishing and its discards (Neves et al. 2006; Arizaga et al. 2009; Plaza and Lambertucci 2017). However, new waste management systems have restricted gulls access to anthropogenic resources that used to be predictable, abundant and consistent, which has led to major changes in the dynamics of these populations worldwide (Oro et al. 2013).

The Berlengas archipelago, located in the continental platform of mainland Portugal, is an important insular ecosystem, classified as a Natural Reserve since 1981 and included in the World Network of Biosphere Reserves in 2001 (Amado et al. 2007). Placed at a high oceanic productivity zone, these islands provide excellent nesting and foraging conditions for seabirds, including the yellow-legged gull (*Larus michahellis* Naumann, 1840). Historically, the first known estimation of the species population size on the Berlenga island (the largest of the archipelago) was in 1934, when only 1000 breeding adults were counted in a context of an apparently stable population (Lockley 1952; Vicente 1987). However, a few decades later, the population exhibited a clear exponential growth, reaching 44 698 breeding adults in 1994 and becoming one of the yellow-legged gulls' largest colonies in Europe (Morais et al. 1998). It was classified as an overabundant pest due to its negative impacts on most of the island's species, including migratory nesting seabirds (e.g. *Calonectris borealis*) and endemic plants (e.g. *Armeria berlengensis*) (Vidal et al. 1998). Consequently, management programmes were implemented by the Institute for Nature Conservation and Forests (ICNF) (Morais et al. 1998). In a first phase, between 1994 and 1996, the culling of breeding adults was performed using avicides (DRC 1339) during the breeding season (SPEA 2016a). After that, management actions have been directed towards a yearly natality control by egg destruction. According to the ICNF, from 1994 to 2016, the breeding population decreased by 68% (SPEA 2016a).

Although the population decline and egg destruction have occurred simultaneously, it is unknown the extent to which these measures directly contributed to the decrease of the yellow-legged gulls on the Berlenga. In fact, open-air dumps used to be the main source of anthropogenic food for gulls as an easy resource to exploit (Cama et al. 2012; Oro et al. 2013). However, the strategic plan of waste management created in 1997 – PERSU I (National Strategic Plan for Urban Solid Waste) led to the permanent closure of all open-air dumps in Portugal by the end of 2001 (Pascoal 2012). Consequently, their replacement by sanitary landfills likely affected this population because refuse deposited in landfills is ultimately covered, and some type of bird deterrence method is usually associated (e.g. falconry) (Cook et al. 2008; Pascoal 2012). The main goal of this study was to model the Berlenga yellow-legged gull population dynamics, considering potential shifts in the balance between fecundity, mortality, immigration and emigration, triggered by the availability of anthropogenic food sources and management actions. For this, we used demographic data spanning the periods before and after the closure of open-air dumps in Portugal and the effects of culling and egg destruction campaigns. Our specific objectives were as follows: (1) to retrospectively recreate the yellow-legged gull population growth from 1978 to 2016; (2) to compare the population growth from 1978 to 2016 under different management scenarios; (3) to predict the population growth from 2018 to 2040 under different management scenarios; (4) to compare the importance of open-air dumps and gull-specific management actions. By evaluating the extent to which past control measures contributed to the decrease of the yellow-legged gulls and predicting the outcome of future management, we expect to provide guidelines for decision making on the current management of this naturally occurring wild species on the Berlenga Island.

4.3 Methods

4.3.1 Model structure and functioning

The dynamic model was constructed using the STELLA 9.0.3 software to simulate the Berlenga yellow-legged gull population dynamics, based on the species' phenological and demographic traits (Figure 16).

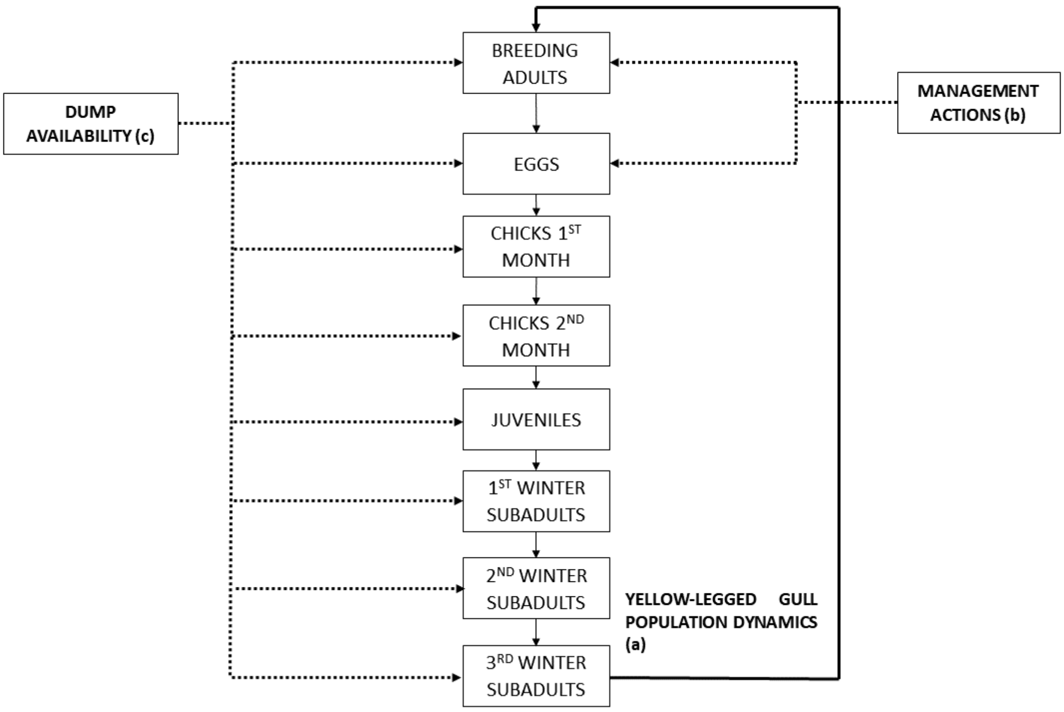


Figure 16 - Conceptual diagram of the dynamic model developed to predict the efficacy of management actions and the influence of dumps availability in the Berlenga' yellow-legged gull population dynamics. The model is composed by different sub-models used to recreate: (a) the yellow-legged gull population dynamics, (b) the influence of management control actions and (c) the influence of extra-anthropogenic food availability (open-air dumps).

In order to incorporate natural individual variability in the model parameterization, the demographic parameters influencing the population dynamics were generated as random values within realistic limits described in bibliographic sources (Appendix L). Full explanations on the model implementation (Appendix M), parameters (Appendix L) and equations (Appendix N) used in the model construction are available in Supporting Information.

The time unit chosen was the month, considered appropriate to model the influence of control measures in the species-specific phenological life stages (e.g. eggs). The simulation extent was designed to start in 1978 and to finish in 2040 in order to assess the long-term impact of management actions and food availability according to retrospective and prospective scenarios (see ’Simulation scenarios’). To recreate the complete breeding cycle of the yellow-legged gull, five life-stages were considered: eggs, chicks (first and second months), juveniles, subadults (first, second and third winter) and breeding adults (Figure 16a; Appendix M). The dynamics of each life stage resulted from inflow and outflow processes related to recruitment, natural mortality, dispersal and reproduction, as well as the effects induced by management actions (Appendix M). These processes were inserted into the model through species-specific phenological and demographic parameters, such as clutch size, hatching success, fledging success and survival rates of juveniles, subadults and adults (Appendix L). Since the model runs on a monthly basis, all rates coming from original measurements other than a month were converted for this specific time scale (Appendix M).

In particular, the yellow-legged gulls lay their eggs between April and May of each year and the incubation lasts for one month (Rainha 1996) (Appendix M). Chick survival results from the dynamic balance between eggs successfully hatched, assuming unviable eggs due to natural causes, and the natural mortality of chicks (Appendix M). Chicks fledge after 2 months (Rainha 1996), remaining as juveniles until the beginning of the first winter (December) when they become first-winter subadults (Appendix M). Subadults transit between life stages (first-winter, second-winter and third-winter) in December, and reach sexual maturity at the age of four years, assuming the average described for the species (Coulson et al. 1982; Morais et al. 1998; Serra et al. 2016). At this stage, birds enter the breeding population. The mortality of juveniles was estimated based on the yearly survival of first-year birds (inverse calculation), the same assumed for first-winter subadults until they reach one year of life (in April of the following year) (Appendix M). Since these birds remain as subadults of first-winter until December, after April, they start being under the mortality rate of birds older than one year (Appendix M).

Food availability has long been suggested to influence seabirds population dynamics through changes in adult survival and fecundity (Lack 1966). In particular, more abundant resources drive an overall increase in individual fitness via alterations in survival (Oro et al. 2013; Steigerwald et al. 2015), egg volume and quality (Bolton 1991; Oro et al. 1999), clutch size (Pons 1992; Pons and Migot 1995; Oro et al. 1999), hatching success (Pons 1992; Oro et al. 1999) and fledging of the young (Pons 1992; Oro et al. 1995; Oro et al. 1999). Therefore, the model was designed to recreate the influence of anthropogenic food sources in the yellow-legged gull population dynamics (Figure 16c), by assuming variation in the species demographic parameters (i.e. clutch size, egg unviability rate and chicks, juveniles and adults mortality rates) between periods of availability and absence of operating open-air dumps (Appendix L) (Appendix M). For this, differences in reproductive parameters were based on relationships between gulls breeding performance and anthropogenic food availability, while changes in survival (of juveniles, sub-adults and adults) were designed according to historical data spanning the periods before and after the closure of open-air dumps in Portugal (Appendix L). Overall, the model is prepared to adjust the period of dump availability throughout the simulation, depending on the scenario considered (see 'Simulation scenarios').

Regarding management (Figure 16b), since campaigns at Berlenga followed the same field protocol every year (culling: 30–40 technicians covered the entire accessible area of the island in predefined transects for 13 days; egg destruction: eight technicians covered the entire accessible area of the island in predefined transects for 3 weeks; SPEA 2016a), the simulated annual effort applied to control actions (expressed in proportion of birds culled or eggs destroyed) was assumed to be constant throughout years. These parameters (annual effort of culling and egg destruction) were defined through calibration, based on the effect of management in the population decline (i.e. the percentage of the breeding population that was reduced between 1994 and 1996 due to culling and between 1999 and 2016 due to egg destruction; SPEA 2016b) (Appendix L). Immigration and emigration were considered as the dynamic balance between the populations size and the Berlenga carrying capacity (Appendix M). Therefore, whenever subadults reach sexual maturity, they are recruited into the breeding population (recruitment). However, if the carrying capacity of the island is surpassed, the exceeding breeding adults are forced to leave the area (dispersal) (Appendix M). The island carrying capacity was assumed as the maximum possible number of nests on the island, considering the average nesting area per breeding pair and the total area of the Berlenga (Luís 1982; Amado et al. 2007; Appendix M).

4.3.2 Initial structure of the population

In order to recreate the structure of the population in 1978, the initial number of breeding adults was 4640 individuals (2320 males and 2320 females), based on the annual censuses compiled by SPEA (2016a). The initial number of eggs, chicks and juveniles was considered 0 since January (the beginning of the simulation) is out of the breeding season. Regarding subadults, the number of third-winter subadults was defined based on the number of birds that were recruited into the breeding population in 1979 (number of recruits in 1979 = number of breeding birds in 1979 - number of breeding birds in 1978), and the survival rate of adult birds (Appendix L) was used to estimate their abundances in 1978 (third-winter subadults = number of recruits in 1979/ adult survival rate). Likewise, the number of second and first-winter subadults was estimated using the adult survival rate for the reverse calculations of their abundances in 1978 (second-winter subadults = number of third-winter subadults in 1978/adult survival rate; first-winter subadults = number of second-winter subadults in 1978/adult survival rate).

4.3.3 Validation

To evaluate the model fit in recreating the yellow-legged gull population growth curve, a baseline scenario was simulated from 1978 to 2016, taking into account the real context and functioning of open-air dumps in Portugal (i.e. until 2001), and the timing of management actions that effectively occurred on the Berlenga Island (i.e. culling from 1994 to 1996 and egg destruction starting in 1999) (see 'Simulation scenarios'). For validation purposes, the number of breeding adults predicted according to the baseline scenario was com- pared with independent real data obtained from annual census (SPEA 2016a). The mean trend of 100 independent simulations was considered in the validation procedure. Simulated data were extracted for the time frame corresponding to the month when censuses were performed (i.e. in June, except for years of culling when censuses occurred in May). A regression analysis (MODEL II) was performed, and the 95% confidence intervals for the intercept and the slope of the regression were used to assess the proximity of the simulated values with the independent real values (Sokal and Rohlf 1995). The simulation was considered validated when the MODEL II was statistically significant; the intercept of the common regression line was not statistically different from 0; and the slope of the regression line was not statistically different from 1 (Sokal and Rohlf 1995; Oberdorff et al. 2001; Warton and Weber 2002). For the regression analysis (MODEL II), the 'sma' function from the package 'smatr' (Warton et al. 2012) in the R software was used (R Development Core Team 2019).

4.3.4 Simulation scenarios

To assess the impact of management actions and dump availability in the population dynamics of yellow-legged gulls breeding on the Berlenga Island, two sets of scenarios were considered (retrospective and prospective scenarios) (Table 5).

Table 5 - Scenarios characterization given the time-period in which management actions (culling and egg destruction) and extra-food source availability (open-air dumps) were active throughout simulation (time extent).

Scenario	Time extent	Culling	Egg destruction	Open-air Dumps
Retrospective				
Baseline	1978-2016	1994-1996	1999-2016	1978-2001
Scenario 1	1978-2016	1994-1996	-	1978-2001
Scenario 2	1978-2016	1994-1996	1999-2016	1978-2016
Scenario 3	1978-2016	1994-1996	-	1978-2016
Prospective				
Scenario 4	1978-2040	1994-1996	1999-2040	1978-2001
Scenario 5	1978-2040	1994-1996	1999-2018	1978-2001

The baseline scenario was used as reference for comparisons between scenarios, in terms of the percentage of variation in the population size (number of breeding adults) in June 2016 (the last year with available census data). Since model simulations assume stochasticity in the species demographic parameters (i.e. random selection between values in the parameter realistic range; Appendix L), results present the average and 95% confidence intervals of 100 independent simulations.

4.3.4.1 Retrospective scenarios

To evaluate the effectiveness of fertility control, the first scenario assumes the lack of egg destruction interventions in the study area: Scenario 1 (dump availability until 2001, culling from 1994 to 1996 and lack of eggs destruction) (Table 5). Furthermore, to assess the potential impact of anthropogenic food sources in the effectiveness of management, dump availability was extended: Scenario 2 (dump availability extended until 2016, culling from 1994 to 1996 and egg destruction starting in 1999) (Table 5). A third scenario considered extended dump availability and the lack of egg destruction in order to isolate the effects of extra- food sources in the yellow-legged gull population dynamics: Scenario 3 (dump availability extended until 2016, culling from 1994 to 1996 and absence of egg destruction) (Table 5).

4.3.4.2 Prospective scenarios

To predict the effects of egg destruction in the yellow-legged gull population trends, two future scenarios were considered: the continuation of fertility control until 2040 (Scenario 4), or its interruption in 2018 (Scenario 5) (Table 5). Both scenarios assumed culling between 1994 and 1996, and the end of dump availability in 2001.

4.3.5 Sensitivity analysis

According to Lee et al. (2015), the purpose of a sensitivity analysis is to provide a measure of the model robustness, measuring the sensitivity of the obtained results to changes in parameters, forcing functions and/or sub-models. Local sensitivity analysis was done by one-parameter-at-a-time technique. For this, we changed the demographic parameters with +/-10% and +/-50% variation (Ligmann-Zielinska 2013), using the original input space of all parameters fixed to their mean value (Appendix O). The result represents the percentage of change in the breeding population size (abundance of breeding birds) between simulations with and without variation in the demographic parameter under study, at any given time frame of the simulation. Since the last time frame is a function of process-based and time-dependent changes acting in the state of the system throughout simulation (Jørgensen 2001), variations in the abundance of breeding adults were assessed for June 2016 ($t = 462$) and June 2040 ($t = 750$), the end of the simulation period in the retrospective and prospective scenarios, respectively (see ‘Simulation scenarios’).

4.4 Results

4.4.1 Validation of the yellow-legged gull population dynamics predicted from 1978 to 2016

According to the baseline scenario (Figure 17), the yellow-legged gull population was predicted to increase from 4640 breeding adults in 1978 to 45 705 breeding individuals in

1994 (CI: 45 504; 45 908). Management actions associated with culling (carried out between 1994 and 1996) led to a decrease in the population to 23 906 breeding adults in 1997 (CI: 23 762; 24 051). The population was predicted to decrease slightly in the subsequent 3 years (1997–2000), before increasing again to approximately 31 800 breeders in 2002 (CI: 31 645; 32 080). After 2002, egg destruction contributed to a decrease in the population to 12 548 breeding gulls in 2016 (CI: 12 449; 12 648). Overall, according to the MODEL II regression, the simulation results were validated (standard major axis P = 1.09e-12; slope P = 0.27; intercept P = 0.76), suggesting the satisfactory fit of our predictions in recreating the yellow-legged gull population dynamics from 1978 to 2016 (Figure 17).

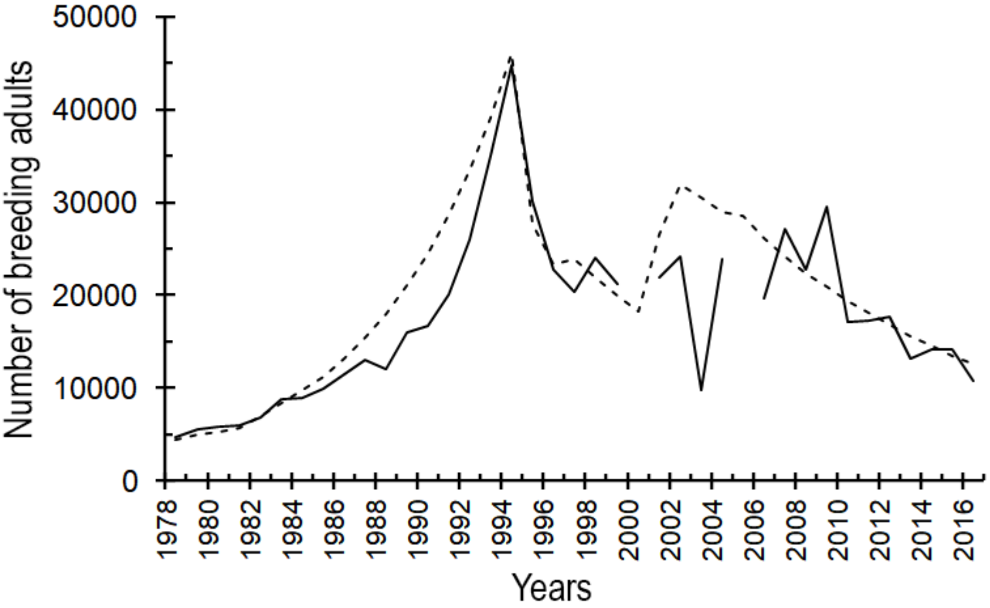
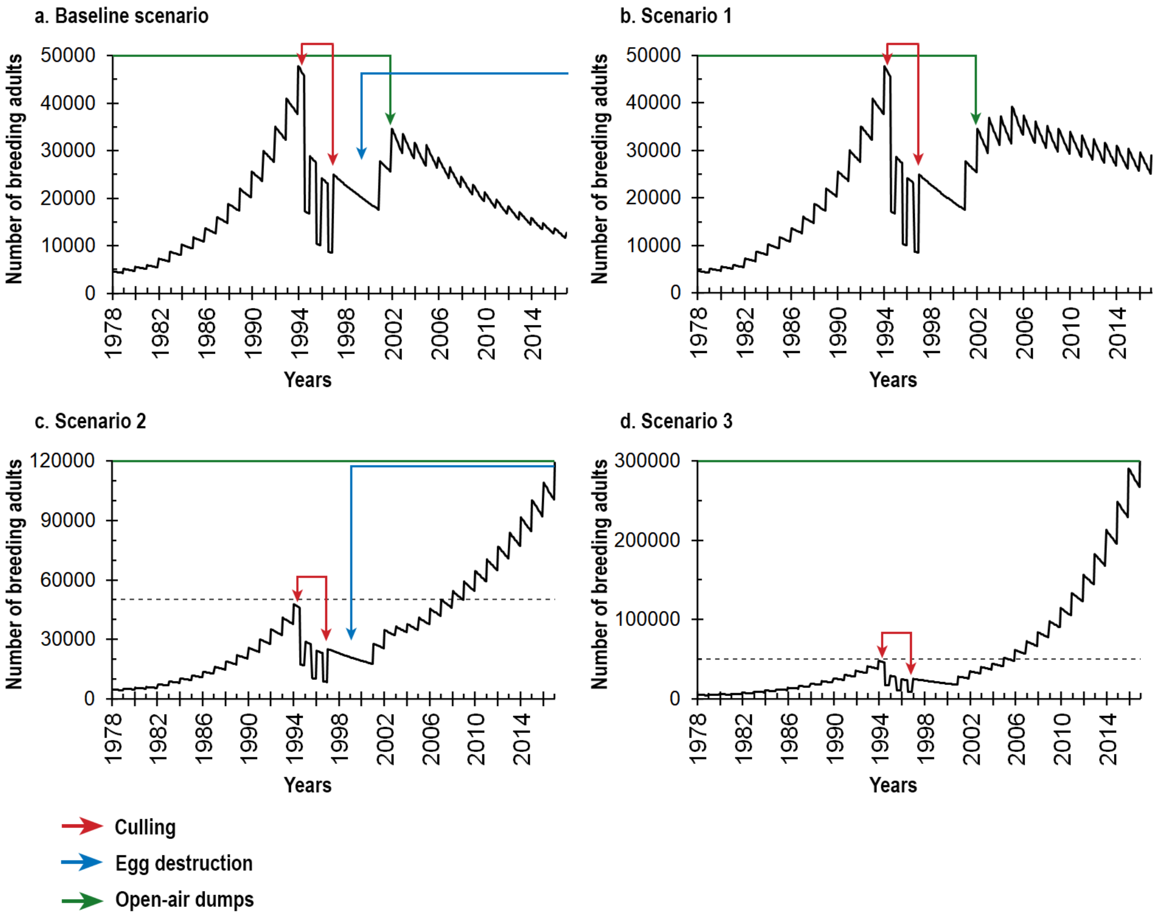


Figure 17 - Trends in the real number of breeding adults obtained from censuses of the yellow-legged gull population on the Berlenga island (continuous line), from 1978 to 2016, and simulated abundances (dotted line; baseline scenario) for the same period (expressed by the coinciding months). Simulation results are presented as the mean of 100 independent simulations.

4.4.2 Comparisons of scenarios

4.4.2.1 Retrospective scenarios

According to Scenario 1 (Figure 18b), in the hypothetical lack of egg destruction, our simulation results indicate that the population followed a similar trend to the baseline scenario until 2003 (Figure 18a), regarding the delay of the effects of egg destruction. Despite the effects of dumps closure in the mortality of adult birds since 2001, after 2003 in the absence of egg destruction, the population was predicted to grow, reaching 35 883 breeding adults in 2005 (CI: 35 595; 36 172). From 2005 onwards, the population decreased to 27 063 breeders in 2016 (CI: 26 824; 27 303) (Figure 18b), due to the influence of dump closure in adults survival and breeding productivity. This represents a population increase of 116% when compared to the reference number of breeding adults for the same year (2016) in the baseline scenario (Figure 18a).



According to Scenario 2 (Figure 18c), the population demonstrated the same trend as the baseline scenario until 2001 (Figure 18a), the year when open-air dumps were permanently closed in the baseline scenario. After 2001, under extended availability of dumps, the breeding population was predicted to grow, reaching 104 463 breeding adults in 2016 (CI: 103 609; 105 317). This represents a population increase of 732% according to the reference number of breeding adults predicted in the baseline scenario for 2016 (Figure 18c). Likewise, the population trajectory in Scenario 3 was similar to the baseline scenario until 2001 (when

Figure 18 - The simulated yellow-legged gull population trends, expressed in number of breeding adults, in response to management actions (culling and egg destruction) and extra-food source availability (dump availability), throughout a period of 38 years (1978-2016). For each scenario considered, the red, blue and green arrows mark the time-period in which culling, egg destruction and open-air dumps were active throughout simulation, respectively. The yellow-legged gull population dynamics are represented by typical yearly fluctuations marked by periods of higher abundance of individuals, after the recruitment phase, and periods of lower abundances as consequence of the natural mortality affecting the population throughout the year. Results are presented as the mean of 100 independent simulations. The horizontal dotted line in scenarios 2 and 3 marks the threshold of 50 000 breeding adults for comparison purposes with the baseline scenario and scenario 1.

dumps were closed) yet, after that the population was predicted to increase exponentially in the lack of fertility control and extended availability of dumps, reaching 277 732 breeding adults in 2016 (CI: 275 428; 280 037) (Figure 18d). This represents a population increase of 2113% (Figure 18d) when compared to the number of breeding adults in the baseline scenario for the same year (Figure 18a).

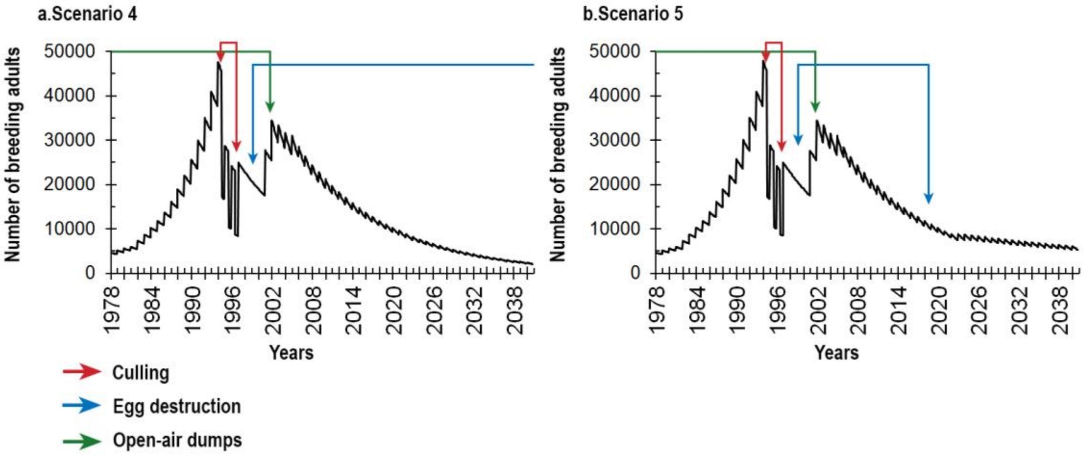


Figure 19 - The simulated yellow-legged gull population trends, expressed in terms of number of breeding adults, in response to management actions (culling and egg destruction) and extra-food source availability (dump availability), throughout a period of 62 years (1978-2040). For each scenario considered, the red, blue and green arrows mark the time-period in which culling, egg destruction and open-air dumps were active throughout simulation, respectively. The yellow-legged gull population dynamics are represented by typical yearly fluctuations marked by periods of higher abundance of individuals, after the recruitment phase, and periods of lower abundances as consequence of the natural mortality affecting the population throughout the year. Results are presented as the mean of 100 independent simulations.

4.4.2.2 Prospective scenarios

The future scenarios assumed the same management actions and dump availability as the baseline scenario until 2018. After that, Scenario 4 considered the maintenance of egg destruction until 2040 (Figure 19a), which caused a considerable decrease of the yellow-legged gull population to 2186 breeding adults in 2040 (CI: 2166; 2205). When assuming the end of fertility control in 2018 (Scenario 5), the population tended to naturally decrease (Figure 19b), reaching 5596 breeding adults in 2040 (CI: 5547; 5645).

4.4.3 Sensitivity analysis

Sensitivity analysis showed that, in the retrospective scenarios, the model was highly sensitive to fluctuations in clutch size and chick mortality in periods of dump availability, while mortality of adult birds was influential during periods of pre- and post-dump closure (Appendix P). In the prospective scenarios, variations in clutch size, chick mortality and adult mortality were influential during periods of pre- and post- dump closure (Appendix P). The model was still sensitive to changes in egg unviability rate after dumps closure in the prospective scenarios (Appendix P). Regarding management actions, the yellow-legged gull breeding population was particularly sensitive to culling intensity in both retrospective and prospective scenarios, while egg destruction effort appeared as a sensitive parameter in the prospective scenario that assumes the continuation of fertility control (Appendix P). In particular, if egg destruction continues indefinitely in the study area (Scenario 4), our results indicate that variations in egg unviability rate, clutch size and adult mortality will be the most influential demographic parameters for the population future decline (Appendix P).

4.5 Discussion

4.5.1 Potential impact of extra-food resources availability in the effectiveness of current management actions

Validation is considered a fundamental requirement to assess the relative accuracy of models response to new contexts, based on comparisons between simulations and independent real data sets (Rykiel 1996). In this study, the validation procedure confirmed the satisfactory model fit in recreating the Berlenga yellow-legged gull population dynamics from 1978 to 2016, allowing to use the baseline scenario as a reference to compare alternative scenarios of management and food availability. Furthermore, the relatively narrow range of variation in model simulations (according to confidence intervals) indicates low model uncertainty, ensuring credibility in the average predictions obtained.

According to our results, the hypothetical lack of fertility control on the Berlenga Island (Scenario 1) produced differences in the trajectory of the yellow-legged gull breeding population when compared with the baseline scenario (considering egg destruction). Despite a slight increase after dumps closure, the population tended to subsequently decrease, albeit at a slower rate than in the baseline scenario. This suggests that in the actual context of management actions and food availability (baseline scenario), egg destruction campaigns contributed to a supplementary population reduction of 54% in 2016. Nevertheless, the closure of dumps seemed to be the most influential factor for the population decline verified at Berlenga, since in the scenario of extended availability of anthropogenic food sources (Scenario 2), egg destruction was not effective in controlling the population growth. Instead, long-term campaigns of fertility control played a role in mitigating the potential impact of open-air dumps (Scenario 2 vs. Scenario 3), only attenuating the influence of extra-food sources in the increase of the population.

These findings are supported by empirical studies showing that the effectiveness of animal management can have limited local effects (Ransom et al. 2013; Koons et al. 2014). In particular, fertility control at Berlenga only started affecting the yellow-legged gull breeding population in 2003, 4 years after the beginning of these measures, when the first affected cohorts were recruited into the population. Consequently, despite the population decrease due to the culling of adult birds, the population tended to recover afterwards, while the effects of fertility control didn't affect the breeding population. These results are consistent with the idea that while intensive culling and fertility control can successfully reduce gull populations (e.g. Blokpoel et al. 1997; Scopel and Diamond 2017), these measures must be maintained continuously so that its effects can last in time (Thomas 1972). This is because, as opportunistic species, gulls' generalist feeding behaviour allows them to adapt foraging strategies depending on the type of resources most readily available (Bosch et al. 1994; Duhem et al. 2003, 2008; Egunez et al. 2018). Therefore, to many opportunistic species with high dispersal abilities, islands borders and/or the limits of natural reserves do not represent physical barriers to prevent the access to anthropogenic resources that continuously promote their populational growth, as well as to individuals from the outside to readily replaced those killed in control programmes via short-term recolonization (e.g. Merrill et al. 2006; Lieury et al. 2015; Beggs et al. 2019).

On the contrary, preventing the accessibility of gulls to anthropogenic resources can trigger a decrease in populations' growth rates (Duhem et al. 2008) by reducing productivity and recruitment, thus promoting shifts in population dynamics (Pons 1992; Oro et al. 1995; Steigerwald et al. 2015). In this perspective, our predictions show that dump closure produced a long-term detrimental effect in the yellow-legged gull demographic parameters after 2001. In particular, despite the instantaneously decrease in the survival of breeding birds, negative consequences were more pronounced after 2005, when the individuals' reduced breeding productivity started affecting the population (i.e. 4 years after dump closure in 2001, when the first affected cohorts were recruited into the breeding population). This suggests that the substitution of open-air dumps for sanitary landfills in Portugal played a key role in restricting the recruitment of new birds into the population, which ultimately limited the yellow-legged gull breeding population size on the Berlenga. Notably, these results are consistent with the causes of expansion between 1978 and 1994, when the population exponential growth coincided with the increased availability of anthropogenic food supplies (e.g. Harris 1970; Duhem et al. 2008; Arizaga et al. 2009).

Overall, our results highlight the role of interactions between local and regional processes in the regulation of population densities and, consequently, in the effectiveness of animal management programmes (Oro 2003). In fact, while culling served to instantaneously reduce gulls density to practical numbers on the Berlenga, the influence of fertility control along with dumps closure appeared to be critical for the verified local decline. Likewise, other studies show that the effectiveness of animal management actions depends on context-specific environmental conditions (e.g. Smith and Carlile 1993; Scopel and Diamond 2017). For instance, the large decrease of the yellow-legged gull population at Dragonera Natural Reserve (Balearic Archipelago, Spain) was attributable to the combined effects of landfill closure and the poisoning of adult birds (Payo-Payo et al. 2015). Therefore, our study supports the idea that controlling the exposure of gulls to human waste is essential to prevent their uncontrolled growth (Huig et al. 2016; Real et al. 2017). In fact, if defined within broader environmental and regional management plans, gull management programmes will be able to control more naturally and efficiently (and consequently with less funding effort) the density of populations in the long run, especially those with potential for expansion given historical and/or actual trends (Runge et al. 2006; Oro and Martínez-Abraín 2007).

4.5.2 Consequences of future management

The last census of the yellow-legged gull population size at Berlenga recorded 10 693 breeding birds in 2016, which resulted from a marked decline in the population size throughout the last 20 years. Even so, future management perspectives point to egg destruction campaigns, at least, until 2024 (SPEA 2019), without a specific target in terms of a minimum threshold for local seagull abundance. In this perspective, if fertility control continues indefinitely in the study area (Scenario 4), our predictions suggest an unprecedented loss of breeding individuals, possibly threatening this population by excessively decreasing its numbers (around 2000 breeding individuals in 2040). Alternatively, if no more management takes place (Scenario 5), the population is projected to decrease around 50% in the next 22 years, tending to similar abundances of that verified before the population exponential growth (around 5500 breeding individuals in 2040). Based on these results, we stress the need of adjusting management practices taking place at Berlenga according to the size and trajectory of the population, so that a compromise between controlling the species and ensuring its future viability can be attained. In fact, according to the model sensitivity, this population seems very sensitive to changes in adult mortality and productivity, regardless of extra-food supply availability. Thus, regular monitoring of variations in adult survival, clutch size, hatching and fledging success is essential to keep the population at sustainable levels (see ’Sensitivity analysis’). For instance, if the adult mortality rate is on average 10% higher than that considered in our predictions, the decision to maintain fertility control can aggravate the future population decline (predicted for Scenario 4) in about 55% (i.e. 1215 individuals in 2040). In this context, reducing fertility control effort (to less than 42% of the eggs destroyed annually) could prevent against potential negative effects related to environmental and demographic variability, thereby ensuring a more controlled stabilization of the population. This is particularly important in the current context of increasing restrictions of seagulls’ access to anthropogenic resources, which may intensify the future decline of yellow-legged gull populations. In fact, gulls can still benefit from food subsidies from landfills and fishing discards however these sources will become more limited in the future due to stricter European legislations and regulatory standards (i.e. the Directive [EU] 2018/850 amending the Directive 1999/31/EC on the landfill of waste and the Regulation [EU] No 1380/2013 aiming to progressively eliminate discards in all Union fisheries). Therefore, ensuring that the Berlenga yellow-legged gull population does not become threatened as consequence of disproportionate control measures is crucial to preserve its future viability and, ultimately, the biological and ecological integrity of the Berlengas Archipelago Natural Reserve.

4.5.3 Sensitivity analysis

According to the sensitivity analysis, model predictions were particularly sensitive to fluctuations in clutch size and chick mortality, especially during periods of dump availability in the retrospective scenarios. These results corroborate the idea that extra-food resources from human origin had a serious effect on the breeding success of yellow-legged gulls, driving major implications in the population trajectory during the last decades. Interestingly, sensitivity analysis pointed to the influence of egg unviability rates in the prospective scenarios, suggesting that in the current context of food availability, new reproductive traits may become influential for future population trajectories, as described in real situations (e.g. Hebert et al. 2020). On the other hand, model results were sensitive to fluctuations in adult mortality in periods of pre- and post-dump closure, in both retrospective and prospective scenarios. In fact, adult survival is a key factor driving long-lived species' population trends (Saether and Bakke 2000). This explains why variations in the intensity of culling appeared determinant to the yellow-legged gull population trends in both types of scenarios; i.e. culling has a direct effect on adult mortality thus having the potential to dramatically change population trends in the short term (Scopel and Diamond 2017). Regarding egg destruction effort, it was influential only if fertility control continues during the next 20 years. This occurred because, since breeding parameters are the target of these measures, it is required more time and continued exposure to produce noticeable effects at the breeding population level (Thomas 1972). Under such conditions, special attention should be given to the effects that fertility control might have in the population future persistence, being essential to identify quantitative management criteria that allow to sustaining a minimum viable population (Brook et al. 2011). We highlight the following demographic thresholds as critical to avoid placing this population in unacceptable danger (i.e. less than 2000 breeding birds in 2040): adult mortality rate 0.21, clutch size 2.26, chick mortality rate 0.9 or egg unviability rate 0.45. These thresholds should be considered individually as all parameters can equally determine the 'turning point' for the referred decline.

4.5.4 Model assumptions and future modelling perspectives

Assumptions are the foundation of any modelling process and are used to bring models closer to the intended reality. In this study, variations in breeding parameters associated with periods of either presence or absence of operating open-air dumps were based on empirical studies that found a direct cause–effect relationship between gulls breeding performance and the availability of anthropogenic food sources (i.e. mainly open-air dumps but also landfills and fishing discards). Regarding variations in adults survival, these were based on population studies of seagulls in the Biscay Gulf before and after 2000 (between 1983 and 1986 and between 2006 and 2013, respectively), when the regulation of open-air dumps was implemented according to European legislation and regulatory standards (i.e. the European Directive 1999/31/EC – Landfill Directive). In this perspective, other factors related to the availability of anthropogenic resources may be indirectly expressed in adult survival rates, such as those associated with local emigration. In fact, a decrease in food supply can trigger the dispersal of individuals, resulting in reductions of apparent survival (true survival + emigration) (Rock and Vaughan 2013). Also, cities are increasingly used by seagulls both as nesting and resting sites due to greater abundance of anthropogenic food sources (Cama et al. 2012; Huig et al. 2016; Goumas et al. 2019), thus representing a potential emergent cause for gulls emigration from natural systems into urban environments (Rock 2005). Our approach therefore provides a useful starting point for the development of more complex models, such as the introduction of other interactions and interferences (e.g. local dispersal, fishing discards and interaction with other species) with precise applicability under increasingly realistic conditions. The model can also be used to assess alternative management scenarios, for instance, to compare the potential effectiveness of culling against egg destruction campaigns and/or the combination of both in the past, as well as in the future for the design of suitable actions targeting upcoming conservation goals.

4.6 Conclusions

This study supports the idea that the permanent closure of open-air dumps in Portugal likely represented the major contribution for the Berlenga yellow-legged gull population decline since 2001. Nevertheless, fertility control campaigns were able to intensify the magnitude of this trend, promoting a supplementary population reduction of 54%. Additionally, we stress the idea that future management actions, if undefined in time, may threaten this population by excessively decreasing its numbers. However, if fertility control stops, the population is predicted to moderately decline in the next two decades. The developed model represents a useful contribution to evaluate the effectiveness of animal management programmes, aiming a compromise between controlling native populations and ensuring their viability in protected areas. We highlight the interplay between model-based research and ecological monitoring to anticipate, with scientific credibility, the ecological consequences associated with the control of wild species, and test the effectiveness of ongoing management programmes.

General Discussion

The chapters of this thesis are complementary contributions to the understanding of individual-level mechanisms shaping shearwaters foraging behaviour during chick rearing. Special emphasis was given to processes related with their sensorial and cognitive capacities to locate prey at sea, and the need to balance the demands of self-feeding and chick provisioning within the constraints imposed by central place foraging. Particularly, this study reveals: 1) a potential link between foraging behaviour and the decision processes associated with timing of nest arrival; 2) a synergistic effect between olfactory foraging and local enhancement for the optimal foraging behaviour of shearwaters; 3) flexible strategies of parental behaviour and cooperation for chick provisioning and foraging decisions; and 4) guidelines for site-specific management programs with implications for the reproductive ecology and conservation of shearwaters.

Although commonly accepted that foraging and provisioning are intrinsically linked mechanisms (Ydenberg 1994; Ydenberg et al. 1994; McNamara and Houston 1997), cause-effect relationships between foraging behaviour and at-night nest attendance patterns of burrow-nesting procellariforms have received poor empirical support. Our results show empirical evidence that Cory's and Cape Verde shearwaters seem to adjust the timing of nest arrival according to variations in oceanographic conditions around breeding sites, suggesting that at-night nest attendance behaviour is a flexible trait that changes in relation to local foraging conditions. To reach these conclusions, the use of environmental remotely-sensed data was determinant to capture inter-annual changes in oceanographic conditions around breeding sites, while GPS tracking data enabled to accurately assess the timing of shearwaters nest arrivals and to characterize foraging trips distance and duration, used as metrics to compare foraging effort among sampled seasons. Furthermore, combining GPS data with astronomical models allowed to characterize light intensity profiles of nest arrivals, which showed that breeding birds were little influenced by moonlight at colonies (e.g. Van Tatenhove et al. 2018; Ravache et al. 2020). Despite this apparent lack of moonlight avoidance at breeding grounds, the use of General Linear Models were particular helpful to uncover temporal correlations between timing of nest arrivals and moonlight conditions throughout the lunar cycle, revealing an evidence of light-mediated patterns of shearwaters nocturnal foraging behaviour (Foraging efficiency' hypothesis; Imber 1975). Therefore, when interpreted from the stand point of the 'Foraging efficiency' hypothesis, our results indicate that breeding shearwaters delay nest arrivals throughout waxing moon nights (i.e. nights with a growing period of moonlight until moonset), possibly because they are forced to increase foraging effort due to reduced accessibility of prey on the moonlit parts of this set of nights (e.g. Klomp and Furness 1992; Mougeot and Bretagnolle 2000). This pattern, however, seems to be disrupted in years of poor oceanographic conditions, when birds enlarge foraging trips in distance and duration, coming ashore earlier and regardless of moonlight conditions. This suggests that changes in timing of nest arrival between years may be associated with shifts in the individuals foraging and provisioning strategies, adjusted to the spatial distribution of resources around breeding sites (Ydenberg and Davis 2010), raising new hypothesis about the individual-level mechanisms that regulate shearwaters nest attendance decisions, e.g. changes in the relative importance of nocturnal foraging for breeding birds returning from functionally different foraging trips (i.e. self-feeding or chick provisioning trips).

The results suggest that an understanding of shearwaters responses to resource availability and distribution is important to gain quantitative insights into the link between parental foraging and chick provisioning patterns. In this regard, spatially-explicit ABMs are ideal to investigate the behaviour of central place foragers because they can integrate the mechanisms through which individuals perceive, learn and adapt to their environment (DeAngelis and Mooij 2005), thus allowing to predict how breeding birds adjust their at-sea behaviour to obtain resources, and how the outcome of foraging decisions may shape nest visiting and chick provisioning (e.g. Langton et al. 2014; Chudzinska et al. 2020). By combining individual-based modelling, remotely sensed predictors of resources availability and movement properties of tracked Cory's shearwaters, our results suggest that a multi-modal foraging strategy (based on olfactory search and local enhancement) produced the most representative patterns of space use from real individuals, confirming the idea that olfactory and visual stimuli should together activate the central cognitive mechanisms involved in shearwaters foraging behaviour (Nevitt 2008). Model outputs also indicate that the individuals' ability to sense olfactory and visual cues increase the probability of successful encounters with feeding opportunities, allowing birds to maximize energy gains (and therefore offspring provisioning rates) over a wide range of local foraging conditions. As future modelling perspectives, we propose to extend the model to spatio-temporal scales greater than one-day foraging trips around breeding sites in order to investigate the interplay between foraging and chick provisioning throughout chick rearing, and ultimately to link foraging behaviour with breeding performance and reproductive dynamics of colonial seabirds (see 'Future research perspectives').

In this perspective, studying *a priori* the decisional processes by which breeding birds determine their levels of chick provisioning effort is fundamental to understand their foraging decisions during chick rearing. In fact, since parental care involves energetic costs, breeding birds must continuously trade-off the investment in their offspring's demands with their own survival (Stearns 1992). However, the nutritional and energetic requirements between adults and their offspring should differ (Murphy 1996), and therefore decisions regarding foraging grounds and prey types must be considered in the light of these trade-offs, i.e. investing in themselves or caring for their young (Ydenberg et al. 1994). Furthermore, foraging allocation decisions may not depend only in each parent's physiological state or condition, but also in the chick energetic requirements (e.g. Weimerskirch et al. 1997; Granadeiro et al. 2000; Ochi et al. 2009) and in the partner capacity to share the demands of bi-parental care (e.g. Tyson et al. 2017; Wojczulanis-Jakubas et al. 2018). Our results suggest that the ability to regulate provisioning according to the chick's needs allows breeding shearwaters to minimize reproductive costs under better foraging conditions (e.g. Ochi et al. 2016). Furthermore, rather than trying to minimize the cost of parental care solely for themselves (partial cooperative behaviour), a full cooperative strategy seems to enable parents to maximize the survival of their offspring while minimizing energetic costs to themselves, buffering the effects of sub-optimal environmental conditions. Under severe scarcity of resources, the challenge of self-maintenance seems to impair the ability of parents to regulate provision according to the remaining family members, indicating that parental decisions are likely flexible responses to local foraging conditions (e.g. Grissot et al. 2019). Combined, these results suggest that provisioning strategies involving adaptive compromises among the three family members enable breeding individuals to maximize their fitness under variable environmental contexts, and that variation in the strength of these compromises (driven by the parents' foraging efficiency) is an important driver of shearwaters foraging behaviour during this highly demanding phase of its reproductive cycle. The outcomes of this study present important contributions to link foraging behaviour with individual fitness of central place foragers, thus providing essential information to predict shearwaters demographic responses to environmental and trophic changes in the North Atlantic Ocean, including those related with anthropogenic-mediated pressures at breeding sites (see 'Future research perspectives').

In fact, human activities can have a profound impact on the natural world because they drive changes in the strength and nature of interactions between species, leading to ecological imbalances that affect entire ecological networks (Wong et al. 2015). In this study we show the consequences of human-induced environmental changes for the yellow-legged gull population dynamics in the Berlenga archipelago, where this species exerts predatory pressure on eggs of Cory's shearwaters (Lecoq et al. 2010, 2011). Our results suggest that the proliferation of open-air dumps in urban coastal areas was likely the major driver for the yellow-legged gull exponential growth in these islands, where the population reached about 44 000 individuals in 1994, thus creating a severe ecological pressure in this Biosphere Reserve (Vidal et al. 1998). After that, the population started decreasing but, despite the contribution of conservation programs involving the culling and fertility control of adult birds, our results suggest that the permanent closure of open-air dumps in 2001 was the most determinant influence for the species local decline. In the current context of restricted anthropogenic food sources, model predictions suggest that the tendency of the population is to naturally decline. Thus, continuing fertility control campaigns can compromise the future viability of the yellow-legged gull population on the Berlengas Natural Reserve. The developed model still enabled to identify quantitative management criteria (i.e. demographic thresholds) to sustain a minimum viable population, so that a compromise between controlling the excessive population growth of this native species and maintaining its viability in protected areas can be achieved; in this case, by preventing that the Berlenga yellow-legged gull population become severely affected as a consequence of disproportionate control measures.

Overall, this study highlights the interplay between model-based research and long-term empirical studies to investigate the behavioural mechanisms through which seabirds responde to their environment, thus providing the basis to predict population responses to climate- and/or human-induced environmental changes (see 'Future research perspective'). In this perspective, this kind of approaches can be used to support strategic options for impact mitigation and conservation management, by providing projections of indicator trends under realistic social-ecological change scenarios (e.g. Bastos et al. 2016b; Nabe-Nielsen et al. 2018). On the other hand, model-based predictions can also be used to guide and improve the strategic monitoring of key populations, by offering insights into future data gathering efforts for the evaluation of environmental change on their behavioural ecology and population dynamics (Jovani and Grimm 2008, Zurell et al. 2010). In this way, predictive modelling tools can contribute to an increasing efficiency and usefulness of empirical results for assessing and mitigating environmental deterioration, whereas strategic data collection can provide robust datasets to validate models and improve their predictive power (Bastos et al. 2016a).

Future Research perspectives

A modelling framework linking seabirds foraging behaviour to population level processes and conservation

The fact that the most immediate response of animals to environmental change is at the behavioural level places behavioural ecology in a central position to inform natural resource management (Berger-Tal et al. 2011; Wong et al. 2015). Currently, conservation managers are confronting relentlessly increasing pressure to cope with environmental changing conditions. However, establish the link between individual behaviour and population-level processes, the focus of conservation, remains challenging (Bro-Jørgensen et al. 2019). In this section, I discuss the fundamentals underlying a modelling framework that aims to use information about seabirds foraging behaviour and ecology into the conservation of marine species and habitats, providing conceptual and technical advances for its future implementation using the Cory's shearwater as a target model species (see section below: ‘From theoretical considerations to practical implementation: predicting Cory’s shearwaters responses to environmental changes in the North Atlantic Ocean’). The proposal is based on the assumption that modelling the interplay between individual's foraging behaviour and breeding performance in spatially-explicit seascapes is a key step to anticipate seabirds demographic and spatial responses to new environmental and trophic conditions. This will allow evaluating the role of behavioural flexibility in the ability of individuals to cope with climate changes, namely by predicting how individual responses span into population-level effects, thereby providing essential information in supporting decision-making for the management of marine ecosystems.

Population models have long played a central role in the research fields of ecology and conservation biology, allowing to understand, explain, and predict the dynamics of biological populations (e.g. Vargas et al. 2007; Jenouvrier et al. 2009; 2018; Schaub et al. 2010; Bastos et al. 2016a). These approaches assume that changes in populations’ size and structure over time is a consequence of variations in the individuals’ survival and reproduction, triggered by external factors that affect these parameters. In terms of management, these models are useful to assess the ecological status of a population, evaluate causes of population declines or exponential growth, designing management targets, and infer a population’s likely responses to alternative management scenarios (Caswell 2001). The case of the Berlenga yellow-legged gull population model (Chapter 4) is a practical example of the applicability of population models to the management and conservation of target species. In particular, this model proved to be a valuable contribution in the development of a mechanistic understanding of the yellow-legged gull population dynamics, as well as in the evaluation of the effectiveness of culling and fertility control in population trends, and in the definition of targets for the current management of this population. The downside of this approach, however, is that it lacks a mechanistic representation of the ecological processes that gave rise to shifts in the yellow-legged gull demographic traits. Such limitation impairs the model ability to reliably extrapolate outside of the environmental range in which the data were collected (e.g. under changing European legislations and regulatory standards) since the representation of demography in response to environmental variables is constrained by the input data (Evans 2012).

From other perspective, modelling frameworks that incorporate individual-level mechanisms are ideal for generating more informed predictions of population responses to novel environments in the future. In such approaches, demographic trends emerge from individual processes (physiology, behaviour, and evolution) and the interactions between them (Johnston et al. 2019), thus allowing to represent the bottom-up mechanisms that give rise to population dynamics in novel environmental and management scenarios (Grimm and Berger 2016; Stillman et al. 2015). For example, in Chapter 3, I present a behaviour-based model that explicitly incorporates an energetic description of survival and reproduction. The core concept of this model is that shearwater’s reproductive effort results from allocation decisions (life-history traits) that depend on the foraging performance of individuals (physiology) and behavioural interaction among family members (i.e. the focal bird, its pair and their chick). This allows to explore the interplay between parental behaviour and optimal energy allocation decisions in different environments, and predict consequences for individual survival (e.g. adults’ body condition) and breeding performance (e.g. chick growth). Therefore, based on this approach, seabirds demographic trends (i.e. breeding productivity) arise from mechanisms that are based on key principles, like fitness seeking and energy budgets, and thus can be estimated in relation to novel environmental conditions.

Also important when predicting seabird responses to environmental changes is to understand how variations in spatial processes (e.g. changes in foraging distribution) may affect demographic and population trajectories (e.g. Bost et al. 2015). For this, integrating seabird movement behaviour is fundamental to link foraging behaviour with space use patterns and individual fitness (e.g. reproductive success). In Chapter 2, I show the applicability of a spatially explicit ABM to assess the fitness consequences of alternative searching mechanisms potentially used by shearwaters to find prey, which allowed to evaluate adaptive strategies that enable individuals to maximize their fitness under contrasting environmental conditions. Model outcomes provide a mechanistic understanding of space use by Cory’s shearwaters during local foraging trips around breeding sites, linking small-scale patch selection and short-term measures of performance, such as energy gained from the environment per unit time (Stephens and Krebs 1986). This approach has also the potential to establish fitness–habitat relationships at larger scales using individual-based components of fitness, such as survival and short-term reproductive success (McGarigal et al. 2016). In fact, habitat selection decisions during the chick rearing season are expected to emerge from variations in the individuals internal state and in their motivations to alternate between fitness-related activities (i.e. self-feeding or chick provisioning), for which ideal foraging grounds may vary (e.g. Ydenberg and Davis 2010). Besides, different levels of parental effort triggered by variations in prey abundance and distribution have implications for adult body condition and chick growth rate (e.g. Chapter 3). Therefore, being able to couple movement behaviour with allocation decisions at the individual level will allow to investigate the links between foraging efficiency, space use patterns and individual fitness, and ultimately the links between the environment, demographic trends and population changes (Morales et al. 2010).

From theoretical considerations to practical implementation: predicting Cory’s shearwaters responses to environmental changes in the North Atlantic Ocean

Climate change is expected to severely impact marine ecosystems however predicting its consequences across multiple levels of ocean biological organization and function is complex and challenging. In this regard, I propose a modelling approach to anticipate the responses of top predators to novel environmental conditions, using the Cory’s shearwater as a key species. In fact, being an upper-trophic level consumer and wide-ranging pelagic seabird, the Cory’s shearwater is considered an indicator species of broad-scale marine environmental changes in the North Atlantic Ocean (e.g. Paiva et al. 2017; Avalos et al. 2017; Pereira et al. 2020). According to findings in Chapter 1, Cory’s and Cape Verde shearwaters adjust foraging and nest attendance behaviour in relation to variations in oceanographic conditions, confirming the idea that shearwaters are sensitive to the prevailing foraging conditions and thus provide important insights into ecosystems status and change. Therefore, variations in shearwaters behavioural traits, space use patterns and demographic trends can facilitate the diagnosis of climate-driven ecosystems changes, providing a framework to evaluate how future conditions may alter the dynamics of pelagic habitats in the North Atlantic.

In practice, the modelling approach is based on a spatially explicit individual-based model that considers cognitive and social mechanisms potentially used by shearwaters to find resources (Chapter 2). Upon appropriate parameterization of resources abundance and distribution across the landscape (see 'Integration with background environmental data' for further discussion on this topic), model simulations will allow to predict daily energy gains of breeding individuals, thereby providing the foundation to stablish the interaction between energy acquisition and allocation of foraging effort in fitness-related activities, such as self-feeding and chick provisioning. This interdependence can be mediated through the integration of optimal energy allocation decisions that consider the balance between adults' body condition, energetic requirements of their chick, and the interplay between breeding pairs throughout the chick rearing season (Chapter 3). Therefore, the incorporation of dynamic oceanographic conditions will lead to the emergence of behavioural decisions with consequences on trip duration, chick meal size and provisioning rates and, ultimately, chick growth and breeding success. Furthermore, this approach can also benefit from the inclusion of other mechanisms. For example, integrating additional searching mechanisms used by shearwaters, such as those relying on private information from short-term recall and memory (e.g. Paiva et al. 2010c), will improve model's realism in capturing individual choices about how to interact with resource abundance and distribution, increasing model accuracy in quantifying net energy gain by individuals in dynamic environmental scenarios. Since individual organisms constitute the key element of populations, the model will ultimately upscale individual processes into population-level effects, i.e. through density regulatory mechanisms in reproductive success as a function of resource availability (seascape carrying capacity) and behavioural interaction among individuals (intra-specific competition and/or cooperation). In this sense, although the approach is conceptualized for the chick rearing phase, it can be extended to the pre-laying and incubation periods (mediated by the inclusion of stage-specific breeding behaviours) in order to evaluate the influence of resources availability in the regulation of shearwaters breeding dynamics and fitness–habitat relationships throughout the entire reproductive season.

Upon integration with future scenarios of climate-driven oceanographic changes (e.g. warming-induced changes in oceanic physical forcing with consequences in nutrient availability and bottom-up control on food chains), this approach will allow to better understand the fine-scale mechanisms linking climate, oceanographic processes and shearwaters foraging behaviour, spatial ecology and breeding dynamics. In this way, modelling outputs can have direct implication for the process of delineating key pelagic habitats, because in addition to determining shearwaters habitat use patterns, they also involve the analysis of future habitat-linked population demographics under scenarios of change (McLane et al. 2011). Besides, since individual fitness emerge from allocation mechanisms that are based on key principles of life history theory, the same decision rules can be used for different species (within the same functional group), differing only in parameterization, i.e. the modelling framework is extensible to other species and geographic locations. Therefore, I hypothesize that the proposed framework will enable the identification of priority conservation areas for the protection of marine populations, communities, and ecosystems, thereby supporting the definition of future conservation measures for Cory's shearwaters in particular and for the North Atlantic in general.

Finally, due to its modular structure, the framework can be adjusted and refined to include physiological and behavioural responses to other climate-related stressors (e.g. increasing air temperatures and frequency of heat waves; Cook et al. 2020), thus providing a more complete assessment of the full effects of climate change on seabirds. Furthermore, although this proposal was designed to explore the role of habitat quality in breeding productivity, the model could also be extended to study the influence of environmental drivers in other demographic traits, namely adults' survival at over-wintering sites or across the entire annual cycle of Cory's shearwaters. Also interesting could be including direct mortality sources of breeding birds and of their offspring, such as those caused by accidental bycatch and nest predation, respectively. This could be useful to evaluate the cumulative influence of climate-induced and human-related pressures in shearwaters breeding populations, especially for those that may be more vulnerable to perturbation due to their small population size and breeding distribution area, such as the endemic Cape Verde shearwater.

Integration with background environmental data

A key step for the conceptualization of spatially explicit individual-based models is the representation of the environment with which individuals interact (Bian 2003). In this regard, ocean circulation models provide historical estimates and forecast predictions of relevant oceanographic variables (e.g. CHL and SST, salinity, and mixed layer depth) at spatio-temporal resolutions capable of integrating shearwater responses to fluctuations in resource availability throughout the breeding season (e.g. daily resolution and 10 km pixel resolution) (e.g. Lellouche et al. 2018). Furthermore, coupling ocean models with atmospheric forcing from climate models (using advanced dynamical high-resolution downscaling techniques) allow to project ocean states according to climate change scenarios (e.g. Pires et al. 2016; Fagundes et al. 2020), recreating high resolution information that enable to investigate the foraging behaviour of seabirds in very dynamic environmental contexts. However, despite the usefulness of projecting an array of variables that characterize the ocean physical and biogeochemical properties at unprecedent scales, understanding seabird-foraging habitat associations is fundamental to identify areas of trophic interactions between individuals and the pelagic realm. For example, owing to the difficulty in obtaining and/or predicting direct measures of prey data fields in marine ecosystems, CHL and SST can be used as useful proxies for marine productivity (i.e. prey abundance) (Grecian et al. 2016; Serratosa et al. 2020). Yet, although resource availability is often assumed to be correlated with food abundance, it also reflects the ease with which seabirds can access prey (e.g. Boyd et al. 2015). Therefore, identifying the ocean physical processes that promote the accessibility of prey to seabirds, including the variables that best describe them, is essential to project variations in resource availability and distribution across the seascape.

In this regard, I propose to bring the Landscape Ecology paradigm into the study of pelagic systems in order to investigate the role of pelagic landscape structure and function in seabird habitat-associations at large spatial scales. In particular, I hypothesize that the identification of oceanographic variables influencing shearwater occurrence patterns across different spatio-temporal scales will improve the creation of habitat suitability maps (i.e. using multi-scale habitat suitability models; Bellamy et al. 2020) that can be integrated as background information in the approach outlined above (see ‘From theoretical considerations to practical implementation: predicting Cory’s shearwaters responses to ecosystem changes in the North Atlantic Ocean’). For example, as part of an exploratory research, I tested whether explicit metrics of the pelagic seascape can be used to explain Cory’s shearwaters space use patterns during long foraging trips around the Corvo island (Azores) (Figure 20). For this, I used an index of foraging effort (based on a 10-days composite of Cory’s shearwaters GPS tracking data in August of 2010; 16 individuals and 5-min GPS data) addressed at two candidate spatial scales (average time foraging/individual in grid cells of 50x50km and 100x100 km) (Figure 20). This index was overlaid onto oceanographic structures such as mesoscale eddies and filaments, identified through Eularian (grid-like:

okubo weiss parameter derived from sea surface high datasets; Douglass and Richman 2015) and Lagrangian (particle-like: Finite size Lyapunove exponent derived from marine surface velocity data; d 'Ovidio et al. 2004) diagnostics of horizontal ocean circulation in the North Atlantic region (Figure 20).

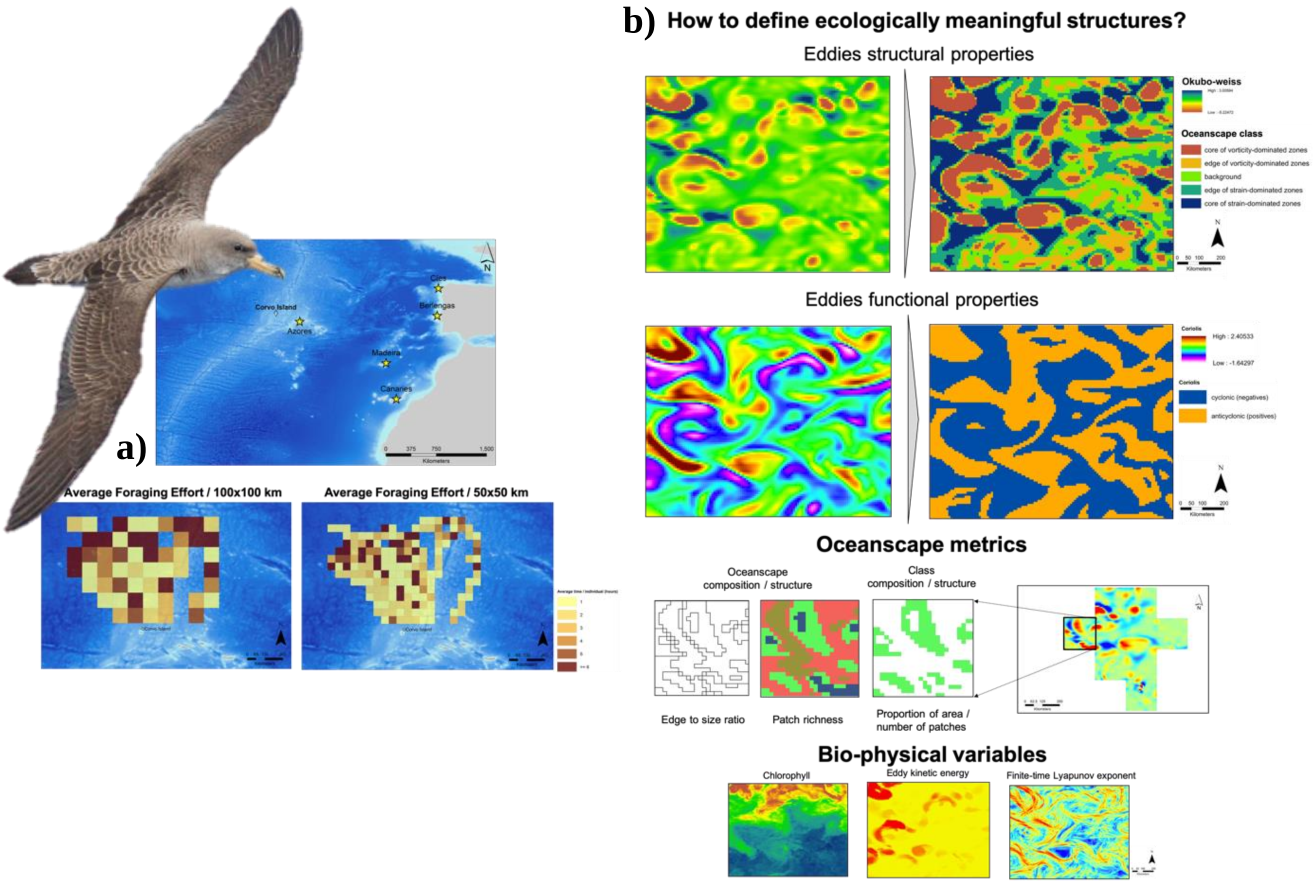


Figure 20 - a) Index of Cory's shearwaters foraging effort addressed at two spatial scales (average hours foraging/individual in grid cells of 50x50km and 100x100 km), obtained from long foraging trips (≥4 days) of breeding individuals tracked between 10 and 20 of August 2010 in Corvo; b) Measures of the pelagic seascape composition and configuration to assess the role of spatial heterogeneity in determining Cory's shearwaters habitat selection.

Compositional classes of eddies' structure (i.e. eddy sub-regions: vorticity-dominated core/edge areas and strain-dominated core/edge areas; Isern-Fontanet et al. 2003) and motion (i.e. cyclonic or anticyclonic rotation; Gaube et al. 2015) were identified in order to explore the role of landscape function in shearwaters habitat preferences (Figure 20). These layers were then used to test for relationships (Multi-model Inference; Burnham and Anderson 2002) between foraging effort and a suit of explicit measures for the pelagic landscape composition (i.e. number of patches and proportion of eddies sub-regions) and configuration (i.e. patch richness and fragmentation), including gradients of bio-physical spatial heterogeneity (i.e. range of: Chlorophyll, Wind stress curl, Eddie kinetic activity and Finite-time Lyapunove exponent) (Figure 20). Preliminary outputs point the 100x100 km resolution as the scale at which emergent patterns of Cory's shearwater foraging effort are best explained by the seascape metrics and variables considered (R^2adj.=0.15/50x50km; R^2adj.=0.45/100x100km). At this scale (100x100km resolution) birds tend to invest more time foraging in cyclonic zones (areas of positive wind stress curl), where the rotation of the oceanic currents is stable in terms of direction (less range in wind stress curl), selecting the interior of eddies (i.e. vorticity-dominated areas), both in proportion of area and number of patches. These results are consistent with the idea that cyclonic eddies in the Northern Hemisphere drive vertical upwelling of nutrients at their interior, typically supporting food webs with high trophic levels (Condie and Condie 2016). Furthermore, since strong eddy activity is responsible of fuelling blooms, promoting the formation of patches with biological enhanced productivity that are spread through horizontal stirring (Chow et al. 2017), the presence of zones dominated by intense strain flow (i.e. great proportion of strain-dominated core areas) at the confluence of energetic eddies in the study area are also important foraging grounds for Cory's shearwaters.

Overall, this approach seems useful to identify the scale at which different predictors interact to produce optimal foraging grounds for shearwaters, thereby providing information that can be integrated into habitat suitability models to create dynamic and spatially explicit projections of resource abundance and distribution across the North Atlantic Ocean. In fact, as advocated by other studies, sequential multi-level methodologies assuming that local environment characteristics are constrained by regional conditions set at higher levels can provide more realistic and nuanced projections of species-environment relationships (Bastos et al. 2016c; 2018; Bellamy et al. 2020). Furthermore, this approach can also help in identifying other variables associated with the suitability of foraging grounds for shearwaters at finer scales (e.g. driven by sub-mesoscale physical forcing). Therefore, I suggest the integration of multi-scale habitat suitability maps (created from ocean modelling and climate projections) into spatially explicit ABMs as a promising avenue to study the interplay between climate, oceanographic conditions (including resources abundance and composition through integration with prey data; e.g. Triantafyllou et al. 2019; Boyd et al. 2020), and the population ecology of shearwaters breeding in the North Atlantic Ocean. Undoubtedly, the development of such innovative proposal will be a future stimulating research line, while simultaneously promoting an integrated approach to test the applicability of the Landscape Ecology paradigm into the study of pelagic systems (Jelinski 2015).

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Supplementary Material

Chapter 1

Appendix A - Fieldwork characterization in each studied colony and monitoring year, including fieldwork period, GPS time interval, number of tracked birds, number of foraging trips/arrival events, total number of monitoring nights, number of waning and waxing moon nights, discriminated by moonless (Moon Fraction < 0.5) or moonlit nights (Moon Fraction ≥ 0.5), number of new moon nights, and number of full moon nights. Study colonies of Cory's shearwaters (*Calonectris borealis*) in Berlenga Island (Berlengas archipelago), Corvo Island (Azores archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

	Year	Fieldwork period	GPS time unit (min)	No. tracked birds	No. foraging trips/arrival events	Total no. nights	No. waning nights (Moonless / Moonlit)	No. waxing nights (Moonless / Moonlit)	No. new moon nights	No. full moon nights
Berlenga	2007	30 Aug. – 5 Sept.	5	10	15	7	7 (1/6)	0	0	0
	2010	12 Aug. – 24 Aug.	5	29	132	13	0	12 (5/7)	0	1
	2011	1 Sept. – 11 Sept.	5	10	31	11	0	11 (4/7)	0	0
	2012	5 Sept. – 19 Sept.	5	9	69	15	11 (7/4)	3 (3/0)	1	0
	2013	10 Sept. – 20 Sept.	5	9	38	11	1 (0/1)	9 (3/6)	0	1
	2014	4 Sept. – 13 Sept.	5	8	38	10	4 (0/4)	5 (0/5)	0	1
	2015	3 Sept. – 12 Sept.	5	17	74	10	10 (7/3)	0	0	0
	2016	1 Sept. – 13 Sept.	5	13	67	13	0	12 (8/4)	1	0
	2017	10 Aug. – 7 Sept.	10	27	326	29	12 (5/7)	15 (8/7)	1	1
Corvo	2007	26 Jul. – 10 Aug.	5	7	10	16	11 (5/6)	4 (0/4)	0	1
	2010	1 Aug. – 27 Aug.	5	42	316	27	12 (6/6)	13 (6/7)	1	1
	2015	17 Aug. – 22 Aug.	5	6	11	6	0	6 (6/0)	0	0
	2017	15 Aug. – 13 Sept.	10	10	37	30	13 (5/8)	15 (7/8)	1	1
Porto Santo	2011	5 Aug. – 20 Aug.	5	9	33	16	7 (0/7)	8 (2/6)	0	1
	2012	3 Aug. – 23 Aug.	5	5	20	21	14 (7/7)	6 (6/0)	1	0
	2014	31 Jul. – 12 Aug.	5	5	30	13	2 (2/0)	10 (4/6)	0	1
	2015	29 Jul. – 10 Aug.	5	5	33	13	10 (3/7)	2 (0/2)	0	1
Raso	2013	5 Sept. – 22 Sept.	10	6	55	18	3 (3/0)	13 (7/6)	1	1
	2014	19 Sept. – 2 Oct.	10	4	11	14	5 (5/0)	8 (7/1)	1	0
	2015	19 Sept. – 3 Oct.	5	12	103	15	5 (0/5)	9 (3/6)	0	1
	2017	24 Aug. – 14 Sept.	5/10	21	150	22	8 (1/7)	13 (6/7)	0	1

Appendix B - Dunn’s pairwise pos-hoc multiple comparisons and statistical significance (p-value) (* p<0.05; ** p<0.01; *** p<0.001; **.** p<0.1) for timing of nest arrival and light intensity at burrow entrances among all monitored years per study colony. Study colonies of Cory’s shearwaters (*Calonectris borealis*) in Berlenga Island (Berlengas archipelago), Corvo Island (Azores archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

Timing of nest arrival

Berlenga	**2007**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**
2007		-316.430 (1.3e-05 ***)	-112.981 (1.00)	-50.038 (1.00)	126.850 (1.00)	9.179 (1.00)	-110.650 (1.00)	12.884 (1.00)	-72.688 (1.00)
2010			203.450 (0.00029 ***)	266.393 (1.4e-13 ***)	443.280 (< 2e-16 ***)	325.609 (3.3e-13 ***)	205.780 (1.9e-08 ***)	329.314 (< 2e-16 ***)	243.742 (< 2e-16 ***)
2011				62.943 (1.00)	239.831 (0.00051 ***)	122.160 (0.971)	2.331 (1.00)	125.864 (0.399)	40.292 (1.00)
2012					176.888 (0.00448 **)	59.217 (1.00)	-60.612 (1.00)	62.921 (1.00)	-22.651 (1.00)
2013						-117.671 (0.885)	-237.500 (6.6e-06 ***)	-113.966 (0.501)	-199.538 (1.2e-05 ***)
2014							-119.829 (0.306)	3.705 (1.00)	-81.867 (1.00)
2015								123.534 (0.048 *)	37.962 (1.00)
2016									-85.572 (0.186)
2017									

Corvo	**2007**	**2010**	**2015**	**2017**
2007		22.461 (1.00)	-3.303 (1.00)	-26.194 (1.00)
2010			-25.764 (1.00)	-48.655 (0.056 .)
2015				-22.891 (1.00)
2017				

Porto Santo	**2011**	**2012**	**2014**	**2015**
2011		-17.142 (0.432)	-3.117 (1.00)	-8.454 (1.00)
2012			14.025 (0.891)	8.687 (1.00)
2014				-5.338 (1.00)
2015				

Raso	**2013**	**2014**	**2015**	**2017**
2013		88.262 (0.020 *)	64.460 (0.00028 ***)	37.359 (0.078 .)
2014			-23.802 (1.00)	-50.903 (0.420)
2015				-27.101 (0.111)
2017				

Light Intensity at burrow entrance

Berlenga	2007	2010	2011	2012	2013	2014	2015	2016	2017
2007		-54.708 (1.00)	-161.097 (0.465)	-359.239 (3.4e-08 ***)	-161.684 (0.362)	66.750 (1.00)	-383.770 (1.7e-09 ***)	-254.552 (0.00055 ***)	-281.244 (8.5e-06 ***)
2010			-106.388 (0.348)	-304.531 (< 2e-16 ***)	-106.976 (0.173)	121.458 (0.049 *)	-329.062 (< 2e-16 ***)	-199.844 (3.6e-09 ***)	-226.535 (< 2e-16 ***)
2011				-198.142 (0.00031 ***)	-0.587 (1.00)	227.847 (0.00018 ***)	-222.673 (1.6e-05 ***)	-93.455 (1.00)	-120.147 (0.069 .)
2012					197.555 (7.5e-05 ***)	425.989 (< 2e-16 ***)	-24.531 (1.00)	104.687 (0.110)	77.995 (0.154)
2013						228.434 (4.8e-05 ***)	-222.086 (2.4e-06 ***)	-92.868 (0.952)	-119.560 (0.026 *)
2014							-450.520 (< 2e-16 ***)	-321.302 (5.8e-13 ***)	-347.994 (< 2e-16 ***)
2015								129.218 (0.007 **)	102.526 (0.004 **)
2016									-26.692 (1.00)
2017									

Corvo	2007	2010	2015	2017
2007		-108.565 (0.009 **)	-77.859 (0.521)	-29.749 (1.00)
2010			30.707 (1.00)	78.816 (4.4e-05 ***)
2015				48.109 (0.996)
2017				

Porto Santo	2011	2012	2014	2015
2011		-18.330 (0.303)	-9.930 (1.00)	-23.909 (0.020 *)
2012			8.400 (1.00)	-5.579 (1.00)
2014				-13.979 (0.563)
2015				

Raso	2013	2014	2015	2017
2013		-142.742 (8.6e-06 ***)	-54.035 (0.003 **)	-88.827 (1.1e-08 ***)
2014			88.707 (0.009 **)	53.914 (0.305)
2015				-34.792 (0.013 *)
2017				

Appendix C - Linear mixed-effects outputs for the influence of fixed (MF: Moon fraction; MF*MoonNights: interaction between moon fraction and waning/waxing nights) and random (Bird_id: birds' individual identification) effects on shearwaters' timing of nest arrival throughout the lunar cycle (* p<0.05; ** p<0.01; *** p<0.001). Study colonies of Cory's shearwaters (*Calonectris borealis*) in Berlenga Island (Berlengas archipelago), Corvo Island (Azores archipelago) and Porto Santo Island (Madeira archipelago), and of Cape Verde shearwaters (*Calonectris edwardsii*) in Raso Islet (Cape Verde archipelago).

	Timing of nest arrival:	Timing of nest arrival:	Timing of nest arrival:	Timing of nest arrival:
Good oceanographic conditions:				
Moon fraction: waning moon nights	-0.016	0.044	-0.022	-0.147***
Moon fraction: waxing moon nights	0.060***	0.048*	0.101**	0.084***
Constant	2.236***	1.995***	2.215***	2.385***
Observations	588	294	80	245
Groups (Bird Id)	81	42	15	37
Log Likelihood	112.36	-35.67	6.25	35.63
Akaike Inf. Crit.	-214.72	81.34	-2.50	-61.26
Bayesian Inf. Crit.	-192.86	99.71	9.22	-43.82
Random effects (L ratio)	45.55***	7.06**	0.04	26.25***
Poor oceanographic conditions:				
Moon fraction: waning moon nights	0.158*	-0.212	0.136	-0.432
Moon fraction: waxing moon nights	0.035	0.103	-0.018	0.107
Constant	2.038***	1.977***	2.257***	1.961***
Observations	163	50	33	43
Groups (Bird Id)	33	21	9	6
Log Likelihood	-15.36	-25.44	-3.98	-41.97
Akaike Inf. Crit.	40.73	60.88	17.96	93.94
Bayesian Inf. Crit.	56.11	70.13	24.96	102.38
Random effects (L ratio)	4.10*	4.06*	0.57	0.95

Chapter 2

Appendix D - ODD protocol: The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2010). The model was implemented using the software NetLogo 6.0.1 (Wilensky 1999).

1. Purpose

The purpose of the model is to investigate how different mechanisms (i.e. foraging strategies) influence seabirds' foraging behaviour during local foraging trips around breeding colonies (i.e. small spatio-temporal scales), using the Cory's shearwaters (*Calonectris borealis*) as a test species. We particularly aim to address to what extent olfactory senses and transference of social information through local enhancement produce real patterns of Cory's shearwaters foraging distribution from two breeding sub-colonies settled in the same island (i.e. Corvo Island, Azores, Portugal). For this, virtual individuals with olfactory perception and social learning were confronted with real oceanographic conditions in the North Atlantic Ocean to produce a range of emergent patterns that depend on the choice of foraging decision rules. Additionally, the model was used to assess how different strategies affect the effectiveness of foraging, taking into account hypothetical scenarios of foraging conditions and increasing densities of foraging individuals. Energy scores were used as a proxy of foraging efficiency in terms of time spent on profitable areas.

The model intends to address three main questions:

(1) To what extent the use of olfactory foraging and/or local enhancement reproduce realistic patterns of Cory's shearwater' distribution and space use?

(2) How does the use of olfaction contribute to the efficiency of individuals foraging in different environmental conditions?

(3) What is the complementary role of olfactory information and local enhancement in the effectiveness of foraging across a gradient of foraging conditions around breeding colonies?

2. Entities, state variables and scales

The model includes two types of conceptual entities (1) internally homogeneous patches that compose the modelled seascape and (2) mobile entities corresponding to Cory's shearwater virtual individuals. Patches are cells of a grid defining the habitat suitability (sea or land, including breeding colony location) and profitability (using chlorophyll-a, sea surface temperature and bathymetry as environmental proxies for resources availability). Virtual birds are characterized by state variables related to their position, movement behaviour, senses and energy scores. Table 1 lists all state variables, their ranges and units, including supporting bibliographic sources.

Table 1 - Description of the model's conceptual entities and state variables: patches and virtual birds.

Patches		
State variables	**Description**	**References and data sources**
Identity	Each patch has a unique identification defined by the respective coordinates (pxcor, pycor).	
Size	Each patch has an area of 16 km^2 (4 km × 4 km).	
Typology	Sea, land, colony location.	
Sub-colonies characterization	Sub-colony A (east side): patch 0.5 -0.5. Sub-colony B (west side): patch -0.5 -0.5.	Ceia et al. 2015
Profitability	Profitable patches (yellow), unprofitable patches (blue shades background).	
Chlorophyll-a concentration	[0; 0.35] (mg m^{-3}). Spatial resolution: 0.04° (approx. 4 km). Time resolution: August 2010 (monthly mean).	OceanColor Web: MODIS Aqua (NASA 2017): http://oceancolor.gsfc.nasa.gov/cgi/l3
Sea surface temperature	[0; 28.31] (°C). Spatial resolution: 0.04° (approx. 4 km).	OceanColor Web: MODIS Aqua (NASA 2017):

	Time resolution: August 2010 (monthly mean).	http://oceancolor.gsfc.nasa.gov/cgi/l3
Bathymetry	[0; 4587.11] (m). Spatial resolution: 0.01° (approx. 1 km).	Global Relief Model (Amante and Eakins 2009): http://www.ngdc.noaa.gov/mgg/global/global.html
	Virtual birds	
State variables	**Description**	**References and data sources**
Identity	Each individual has a single identification number.	
Size	0.75 metres of wingspan (0.0001875 of a patch).	Ramos et al. 2009
Sub-colony identification	Individuals A (sub-colony A). Individuals B (sub-colony B).	
Movement coordinates	xcor, ycor position.	
Distance to nest	[0; 384] km, since sub-colonies are located at the centre of the model world.	
Movement behaviour	Area Restricted Search (ARS); Travelling.	
ARS behaviour	True = 1; false = 0.	
Turning angle (Travel/ARS)	Travel [-40°; 40°]; ARS [-180°; -25°] ∪ [25°, 180°]	Real data tracking from Corvo, 2010. (see 6. 'Input data' and 7. 'Submodels: Foraging behaviour' for additional information)
Speed (Travel/ARS)	Travel [10; 80]; ARS [3; 15]; Km/h	Real data tracking from Corvo, 2010. (see 6. 'Input data' and 7. 'Submodels: Foraging behaviour' for additional information)
Olfactory range	Perception distance: up to 20 km Perception angle: 180°.	Distance and angle: Nevitt et al. 2008
Visual range	Perception distance: up to 10 km Perception angle: 148°.	Distance: Thiebault et al. 2014a Angle: Martin and Brooke 1991
Energy score	[0; 120] cumulative energy gains along simulation (1 unit of energy per tick on a profitable patch); energy losses are not comprised.	

The size of each patch corresponds to 16 km^2 (4 x 4 km) and the total seascape represents an area of 589 824 km^2 (768 km × 768 km). The islands that compose the Azores archipelago are represented by patches classified as land, which are unsuitable foraging areas; the Corvo Island is located at the centre of the world (patch 0 0) where two breeding sub-colonies can be settled (i.e. sub-colony A and sub-colony B), individually or simultaneously. The seascape is characterized by environmental data regarding chlorophyll-a concentration (CHL), sea surface temperature (SST) and bathymetry (BAT), from which feeding patches are established upon specific thresholds.

Virtual birds are associated with collectives from sub-colony A or sub-colony B. The size of the virtual Cory's shearwaters is scaled to the patch size, assuming a wing span of 0.75m (Ramos et al. 2009) that corresponds to 0.0001875 of a 4 km pixel. The movement of virtual agents is defined upon two behaviours: Area Restricted Search and Travelling. Virtual birds may have access to olfactory senses and/or social information according to the foraging strategy defined in the beginning of the simulation. Each tick corresponds to 5 minutes, representing the GPS temporal resolution of Cory's shearwaters data tracking (Ceia et al. 2015). Each simulation lasts 10 hours (120 time units), considered a reasonable period to recreate the average period during which Cory's shearwaters allocate foraging activities during a complete day (Ramos et al. 2009; see also Paiva et al. 2013). For each time unit spend on a feeding patch, virtual individuals gain 1 unit of energy. In the end of the simulation, each bird is able to gain up to a maximum 120 units of energy (hereafter, individual energy score).

3. Process overview and scheduling

Before the simulation starts a foraging decision (FD) rule is selected:

FD1: virtual birds foraging without external cues (hereafter, Uninformed Search);

FD2: virtual birds foraging according to an olfactory-based searching strategy (hereafter, Olfactory Search);

FD3: virtual birds interacting with conspecifics through local enhancement (hereafter, Local enhancement);

FD4: virtual birds foraging according to an olfactory-based strategy and interacting with conspecifics through local enhancement (hereafter, Olfactory Search with Local enhancement).

After the Initialization, the following processes will be processed as sub-models:

Set environmental layers (To import-world)
Update world's view and resources availability (To setup-world)
Run the simulation (To go)
Foraging behaviour (To search)
Feeding behaviour (To feed)
Write outputs (To export)

Processes are performed either by the model agents (i.e. 'Foraging behaviour'; 'Feeding behaviour') and by the higher-level observer (i.e. 'Set environmental layers'; 'Update world's view and resources availability'; 'Run the simulation'; 'Writing outputs'). The time is modelled as discrete time steps (5 minutes interval) over which discrete events occur, and the simulation lasts 10 hours (120 time units). Virtual Cory's shearwaters leave the sub-colonies at the beginning of the simulation, which is considered the beginning of a foraging day. Two ways of modelling animal movement were implemented, taking into consideration the movement decisions that may cause the individuals to act on, and react to, the surrounding environment (Nathan et al., 2008): (1) a Correlated-Random Walk (CRW) based on real characteristics of the animal movements and (2) a Biased Correlated-Random Walk (BCRW) based on the CRW approach combined with the individuals' perception of the landscape characteristics and conspecifics' behaviour. The movement of virtual birds is continuous over space. Virtual birds assume a travelling mode while searching over unprofitable patches, whereas performing ARS behaviour when they find a profitable feeding patch (Figure 1). When they percept a feeding patch location through olfactory or social cues, a biased traveling is triggered towards the feeding area. Whenever either olfactory and social information are available, virtual birds tend to follow conspecifics' behaviour, although olfactory cues can also envisage the response (Figure 1). Virtual birds can perceive land and avoid it, which is prioritized over any other movement decision (Cory's shearwaters are rarely seen flying over land during the day; personal observation). One unit of energy is obtained every time step a virtual bird spend on a profitable patch. All state variables are updated as soon as its value is calculated by the respective process (asynchronous updating), and each process is randomly performed by all agents simultaneously. The number of modelled Cory's shearwaters is constant along simulation, as well as the location of feeding patches throughout the seascape.

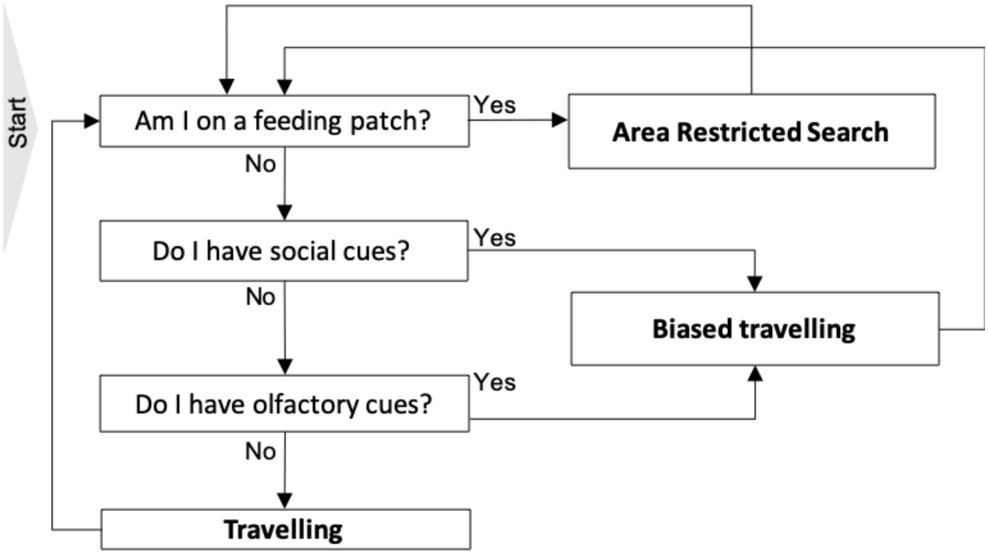


Figure 1 - Conceptual diagram of the virtual Cory´s shearwater' movement behaviour: virtual birds assume a travelling mode while searching for resources throughout the seascape, performing ARS behaviour whenever they find a suitable feeding patch. When virtual birds perceive a feeding area by olfactory or social cues, a biased traveling is triggered towards the identified patch; otherwise virtual individuals travel throughout the seascape solely relying on the information of the patch they are searching in.

4. Design concepts

4.1. Basic principles

To maximize fitness, individuals adopt foraging strategies that provides the most benefit for the lowest energy cost, maximizing net energy gains (Optimal foraging theory; Emlen 1966; MacArthur and Pianka 1966). Seabirds use detailed knowledge of the marine environment in order to optimise foraging efficiency. For this, along with their extraordinary navigation abilities in perceiving their environment through visual and olfactory senses (Sensory-based foraging strategies; Nevitt 2008), sharing of information with conspecifics may also increase accuracy in food resources location (Evans et al. 2016). Mechanisms of social information transfer allow seabirds to update information concerning the location of prey patches through transference of visual information and monitoring of conspecifics' behaviour, such as the congregation of foraging individuals at locations where other individuals are feeding (i.e. adaptation of Recruitment Centre Hypothesis; Local Enhancement Hypothesis; Ward and Zahavi 1973; Mock et al. 1988; Buckley 1997). The local enhancement hypothesis (Mock et al. 1988; Buckley 1997) still suggests that an increase in density, either of conspecifics or in association with other marine predators, improves the probability of encountering food patches thus contributing to increase individual foraging efficiency (Thiebault et al. 2014a,b; Boyd et al. 2016). Both local enhancement and the transfer of information at the colony site have been hypothesized to be the most important mechanisms generating and maintaining specific foraging areas exploited by individuals belonging to the same colony (Wakefield et al. 2013). Consequently, they should also contribute to the spatial segregation of foraging areas between individuals breeding in close colonies, probably as an adaptive mechanism to minimize intraspecific competition for resources (diplomacy Hypothesis; Grémillet et al. 2004).

Correlated-Random Walks (CRWs) emerged in ecology from the analysis of short and middle-scaled animal movement data and provide a standard framework for modelling animal movement and navigation (Bartumeus et al. 2005; Codling et al. 2008). Correlated random walks (CRWs) involve a correlation between successive step orientations, which is termed 'persistence' (Patlak 1953). The relative straightness of the CRW (i.e. degree of directionality) or sinuosity are assumed as relevant properties of the individuals' movement. Thus, CRWs are considered suitable models to reproduce realistic animal movement behaviour (Bartumeus et al. 2005). Paths that contain directional persistence in the movement (i.e. the tendency by animals to continue moving in the same direction) and a consistent bias in a preferred direction or towards a given target are termed biased correlated random walks (BCRWs) (Codling et al. 2008). While in the Uninformed search virtual birds follow a CRW, in the Olfactory search, Local enhancement and in the Olfactory search with Local Enhancement virtual birds use external information (i.e. olfactory and social cues) to target foraging patches, describing a BCRW.

When exploring resources at sea, seabirds must cope with the hierarchical spatial distribution of resources, searching for prey that are clustered from fine to large scale in nested unities (Kotliar and Wiens 1990). 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 appears to be an individual reaction to changes in the resource availability, namely by reducing speed and increase turning rate (i.e. increasing residence time) as a response to increased productivity in a restricted area (Weimerskirch, 2007). Contrarily, when travelling, individuals increase the flight velocity and reduce the turning angle, indicating lower foraging effort associated with a decrease in the residence time on patches (Weimerskirch, 2007). In order to reproduce realistic movement behaviours in the ABM, virtual birds were assumed to describe a travelling mode while searching for resources throughout the seascape (i.e. “flying” over unprofitable patches), whereas performing ARS behaviour whenever they find a suitable feeding patch.

The main goal of the model is to explore the mechanisms underlying seabirds’ optimal foraging behaviour through emergent patterns of individuals’ spatial distribution, foraging at-sea and energy intake (in terms of time spend on profitable patches), including spatial segregation of foraging areas by neighbouring sub-colonies. Model outputs and performance were initially analysed through comparisons between real and simulated data, in order to assess the mechanisms that best described real patterns of Cory’s shearwaters foraging distribution around breeding colonies, using as baseline the study from Ceia et al. (2015). Additionally, the efficiency of virtual individuals using different foraging strategies was analysed taking into account additional hypothetical scenarios of resources availability, along with increasing densities of foraging individuals.

Emergence

The individuals’ spatial distribution and energy intake emerge from their probability of encountering profitable patches, which is expected to vary in complex and unpredictable ways as: (1) individuals have additional cues on the location of feeding patches through olfactory senses and/or social information transfer and (2) the availability of foraging patches and density of foraging individuals change.

Adaptation

Sensorial and social learning increase the fitness of virtual individuals by maximizing net energy gains through increased rates of food resources' encountering. Besides, the movement of virtual individuals reproduce observed behaviours (i.e. travelling and ARS) that are implicitly assumed to indirectly convey individual fitness, since ARS increase residence time over productive patches while travelling minimize residence time over unprofitable areas. Overall, a decrease in foraging ranges and increase in energy gains are indicators of individual fitness and foraging success.

Objectives

The overall objective of virtual birds is to optimise foraging efficiency by spending the maximum time in profitable patches thus maximizing energy gains. Increase in energy intake rates and decrease in foraging ranges are indicators of foraging efficiency.

Sensing

Virtual birds can sense the surrounding environment according to olfactory senses and social information transfer, adapting their movement in response to the available information. Virtual birds have additional cues on the location of feeding patches by precepting the landscape according to olfactory senses up to a maximum of 20 kilometres ahead assuming any wind direction on a 180° perception angle (based on wandering albatross evidence, i.e. Nevitt et al. 2008), which triggers a biased traveling towards suitable feeding areas. Additionally, individuals also interact with each other through visual contact (i.e. local enhancement), using visual acuity up to 10 kilometres (based on Cape gannets evidence, i.e. Thiebault et al. 2014a) on a vision radius of 148° ahead (based on Manx shearwater evidence, i.e. Martin and Brooke 1991). Virtual shearwaters are also able to perceive land through visual perception. At the patch-level, virtual birds adapt their movement behaviour according to the profitability of the patches in which they are foraging in: they assume a travelling mode (i.e. decreasing turning angle and increasing velocity) while searching over unprofitable patches, whereas performing ARS behaviour (i.e. increasing turning angle and decreasing velocity) when they find a suitable feeding patch.

Interaction
Virtual birds interact directly with each other via network foraging. They monitor the behaviour of conspecifics through visual contact to gain information concerning potential foraging patches and feeding opportunities. Therefore, individuals adapt foraging behaviour after detecting other birds foraging on profitable patches (i.e. describing ARS behaviour), adjusting the movement trajectory towards the newly identified patch. This mechanism creates aggregations of foragers feeding on the same patches.

Stochasticity
The movement behaviour of virtual individuals is partially random due to the stochasticity associated with turning angles and flight velocity (i.e. in travelling and ARS). Additionally, it is assumed that at departure from the colony (i.e. in the first 5 minutes) Cory's shearwaters adopt positions exclusively towards the sea (i.e. initial heading of sub-colony A ranges from 45° to 225°, and of sub-colony B ranges from 135° to 315°). Therefore, the initial heading of individuals is randomly determined within specific ranges in order to imply variability in foraging directions while preventing individuals to assume bearings towards land when leaving the colony.

Collectives
Although increasing aggregations of birds can enhance the detectability of larger clusters for other foragers, thus increasing the probability of food encounter (Thiebault et al. 2014a,b; Boyd et al. 2016), the structure of the network was not considered in the modelling procedure.

Observation
Comparisons between real and simulated data were performed to analyse whether each searching strategy (i.e. Uninformed Search, Olfactory Search, Local Enhancement or Olfactory Search with Local Enhancement) reproduce the closest range of patterns observed in real tracked individuals, assuming the average oceanographic conditions around the Corvo Island during August of 2010 (i.e. baseline foraging conditions) (see 5. 'Initialization' for additional information). For this, the response of 20 virtual birds in each sub-colony (the same number of individuals tracked in the study of Ceia et. al. 2015) was simultaneously considered throughout a foraging day, according to each searching strategy. The individuals were randomly selected from a total pool of 1000 virtual individuals (assuming breeders and non-breeders as both contribute to social information transfer), considering a population estimate of 200 breeding pairs for each sub-colony (Ceia et al. 2015) and 6000 breeding pairs for the whole Corvo Island (Oppel et al. 2014). Therefore, for comparison purposes, the following metrics were used (Ceia et al. 2015): (1) maximum distance from colony; (2) bearing from the most distant locations in relation to the colony; (3) geographic position (i.e. latitude and longitude) of foraging areas; (4) 25%, 50% and 75% foraging density areas (km^2), calculated by fixed kernel density (adehabitat package; h = 0.03°; grid = 500) (Calenge 2006). Individual information on virtual birds' identification, sub-colony, distance to nest, heading and movement behaviour (i.e. ARS or travelling) were extracted. ARS points were used to calculate areas of foraging (i.e. geographic position of foraging areas and fixed kernel density areas) (Ceia et al. 2015). Comparisons between real and simulated data were then based on the quantitative assessment of the metrics considered, represented as mean values and standard deviation of the overall pool of foraging trips considered per sub-colony (i.e. 20 virtual individuals). Furthermore, the spatial patterns obtained for each colony and foraging mechanism considered (i.e. 25%, 50%, 75% and 100% fixed kernel density areas) were also inspected. All spatial analyses were performed in ArcGis 10.5 (ESRI 2017).

5. Initialization

The initial state of the model world is defined by environmental layers from which feeding patches are established upon specific thresholds (Table 2). In fact, during August of 2010, Cory's shearwaters tended to forage in areas around the Corvo Island characterized by SST ranging from 23.5 to 24.2 ºC, CHL ranging from

0.06 to 0.1 mg/m3, and bathymetry ranging from 730 and 2112m (Ceia et al. 2015). Therefore, CHA, SST and bathymetry were used to identify foraging patches for virtual Cory's shearwaters foraging in the surroundings of the Corvo Island (Ceia et al. 2015). For this, bathymetry data was extracted from a grid of 0.01° (approx. 1 km) from http://www.ngdc.noaa.gov/mgg/global/global.html (Amante and Eakins 2009), and monthly values of CHL and SST were downloaded from the MODIS Aqua (NASA 2017; http://oceancolor.gsfc.nasa.gov/cgi/l3) at a spatial resolution of 0.04° (approx. 4 km), during August 2010. The obtained layers were then imported into NetLogo and the availability of profitable patches was established by the respective thresholds of CHA, SST and bathymetry, according to Ceia et al. (2015) (hereafter, baseline foraging conditions) (Table 2). Furthermore, in order to assess the effectiveness of foraging mechanisms across a gradient of foraging conditions, two contrasting additional hypothetical scenarios were created, either richer in foraging patches (hereafter, good foraging conditions) or poorer in foraging patches (hereafter, poor foraging conditions) (Figure 2; Table 2). For this, the percentages of profitable patches in the baseline scenario were calculated considering as denominator the total number of patches present in the seascape (36 864 patches). For demonstrative purposes, the scenarios of good and poor foraging conditions considered a relative increment or reduction of circa 50% in that percentage, respectively (Figure 2; Table 2). Initial settings concerning the number of sub-colonies, number of virtual birds per sub-colony, foraging mechanisms and environmental thresholds for classification of profitable patches are displayed in Table 2.

Table 2 - Description of the initial settings for: (i) comparative analyses between real and simulated data and (ii) analyses of foraging efficiency upon contrasting environmental scenarios and density of foraging individual. Specific initial conditions for comparisons with real data were based on empirical data from Ceia et al. (2015), and analyses of foraging efficiency were designed for theoretical experimental purposes. The percentages of profitable patches were calculated considering the total number of patches present in the seascape (36 864 patches).

<table>
<tr><th colspan="8">Initial conditions</th></tr>
<tr><th></th><th>i) Comparative analyses with real data</th><th colspan="6">ii) Comparative analyses of foraging efficiency</th></tr>
<tr><td>Number of birds per sub-colony</td><td>1000 (tracked individuals: 20)</td><td colspan="6">1, 10, 100, 1000</td></tr>
<tr><td>Sub-colonies</td><td>Sub-colony A and B.</td><td colspan="6">Sub-colony B.</td></tr>
<tr><td>Foraging mechanisms</td><td>Uninformed Search
Olfactory Search
Local Enhancement
Olfactory Search with Local Enhancement</td><td colspan="6">Uninformed search
Olfactory search
Local Enhancement
Olfactory Search with Local Enhancement</td></tr>
<tr><td>Chlorophyll-a concentration</td><td>>0.06 mg m^{-3}</td><td rowspan="4"><i>Good Foraging conditions</i></td><td>>0.05 mg m^{-3}</td><td rowspan="4"><i>Baseline foraging conditions</i></td><td>>0.06 mg m^{-3}</td><td rowspan="4"><i>Low foraging conditions</i></td><td>>0.07 mg m^{-3}</td></tr>
<tr><td>Sea surface temperature</td><td>>23.5 °C</td><td>>23.0 °C</td><td>>23.5 °C</td><td>>24.0 °C</td></tr>
<tr><td>Bathymetry (in meter below sea level)</td><td>>730 m</td><td>>720 m</td><td>>730 m</td><td>>740 m</td></tr>
<tr><td>Number of profitable patches (percentage)</td><td>13004 (35.3 %)</td><td>20588
(55.8 %)</td><td>13004
(35.3 %)</td><td>7087
(19.2 %)</td></tr>
</table>

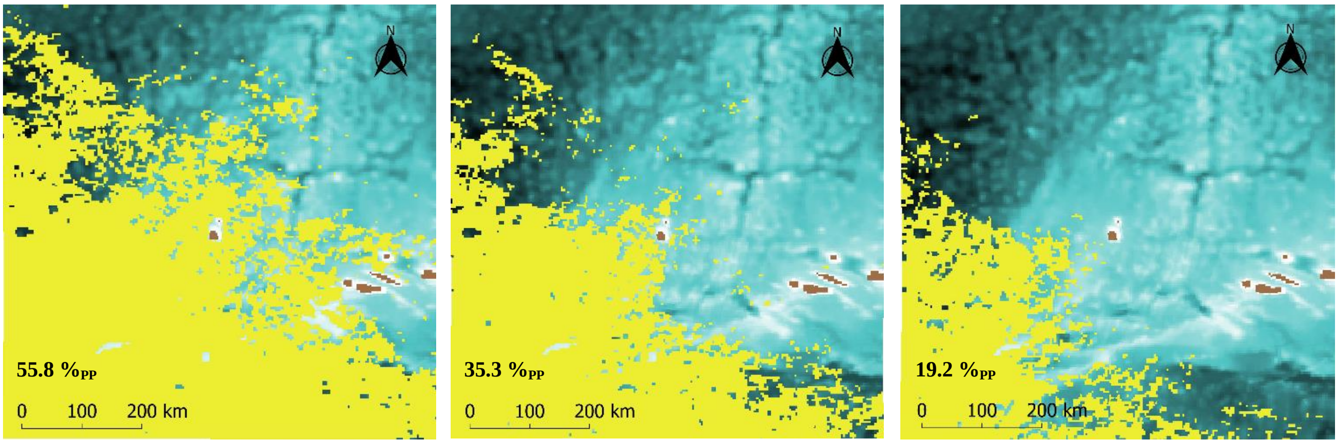
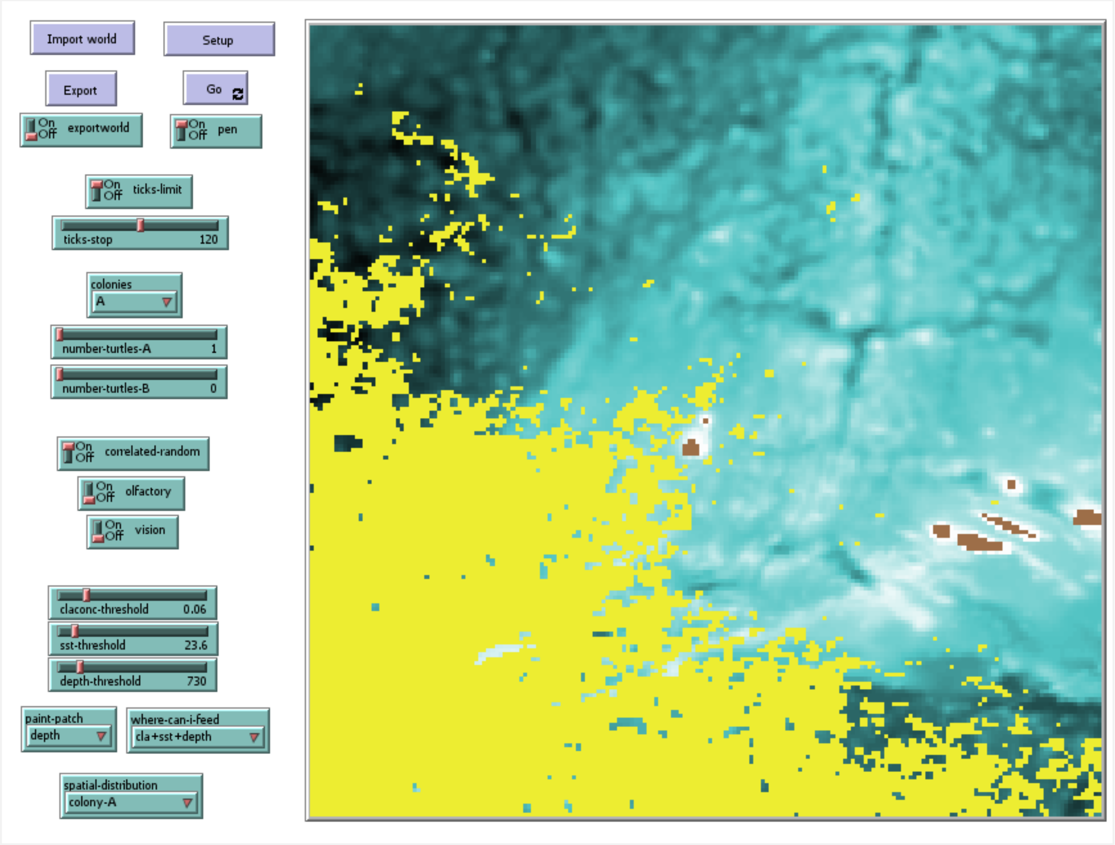


Figure 2 - Cory's shearwater habitat profitability around the Corvo Island, considering three scenarios of foraging conditions: Good foraging conditions (left), Baseline foraging conditions (centre) and Poor foraging conditions (right). Profitable patches are represented in yellow and its relative percentage in the seascape (%$_{PP}$) is displayed in the bottom left corner of each scenario. Islands are represented in brown and the background in blue illustrates bathymetry (darker shades represent increasing bathymetry).

Interface

Settings for the initial model' parameterization and options are displayed in the Interface (Figure 3); the specifications of all commands in the Interface are described in Table 3.



ticks-stop 120

colonies A

number-turtles-A 1

number-turtles-B 0

claconc-threshold 0.06

sst-threshold 23.6

depth-threshold 730

paint-patch depth

where-can-i-feed cla+sst+depth

spatial-distribution colony-A

Figure 3 - The model interface: the world's view and commands associated with initial model settings.

Table 3 - Description of the commands present in the model interface and respective functionalities.

Interface		
Command	**Type**	**Functions**
Import world	Button	To load environmental data (Raster files) into NetLogo.
Setup world	Button	To define the world's view and set up initial model conditions (e.g. feeding patches, number of individuals and respective colonies).
Go	Button	To run the behavioural procedures of virtual birds (e.g. movement and feeding procedures).
Data exportation	Button	To export simulated data as GIS files (.shp) from NetLogo.
Data to export	Switch	To define a pool of individuals for data exportation.
Pen	Switch	To activate *pen-down* of individuals, i.e. to draw the individuals' movement through the seascape.
Simulation extent	Switch	To define an extent for the simulation. If not activated, the simulation doesn't stops.
Length of simulation	Slider	To define the length of the simulation.
Colonies	Chooser	To define sub-colonies: sub-colony A, sub-colony B, or both.
Number-turtles-A	Slider	To define the number of virtual birds from sub-colony A.
Number-turtles-B	Slider	To define the number of virtual birds from sub-colony B.
Uninformed search	Switch	To activate the uninformed search.
Olfactory search	Switch	To activate the olfactory search.
Local enhancement	Switch	To activate local enhancement; must be activated along with the uninformed or olfactory search.
CHL-threshold	Slider	To define a threshold of chlorophyll-a, above which feeding areas are defined.
SST-threshold	Slider	To define a threshold of sea surface temperature, above which feeding areas are defined.
Depth-threshold	Slider	To define a threshold of bathymetry, above which feeding areas are defined.
World's view	Chooser	To select which environmental layer will be displayed on the world's view (upon specific colour scales and range of values): CHA, SST, bathymetry or none
Feeding patches	Chooser	To select which environmental variables' thresholds will be responsible for the characterizations of feeding patches (displayed on the world's view in yellow): chlorophyll-a, sea surface temperature, bathymetry, all variables simultaneously or none.
Foraging patches' density of use	Chooser	To characterize the density of use of feeding areas, to be displayed on the world's view: sub-colony A, sub-colony B or none.

6. Input data

The model use input data to represent time-varying processes associated with the movement behaviour of virtual Cory's shearwaters. To model the movement behaviour of virtual birds, the geometric characteristics of real Cory's shearwater' movements were extracted from daily foraging trips (N=368) around Corvo, during August 2010. This data allowed to assign specific flight characteristics based on the probability distribution of turning angles and flight speeds for two movement behaviours: Area Restricted Search and Travelling. For this, the characterization of Cory's shearwaters at-sea movement behaviours was based on the movement properties of the tracked trajectories for the foraging trips considered, using the Expectation-Maximization binary Clustering (EmbC) algorithm for behavioural classification of movement data, available through the R package ´EmbC´ (Garriga et al. 2016; R Core Team 2017). The EmbC algorithm thus allowed a binary discretization of the shearwaters' tracking data in terms of high/low values of velocity and turning behaviour, enabling to categorize data-points into one of the following behavioural states: area restricted search (i.e. low velocities and high turns) or travelling (i.e. high velocities and low turns). The probability distribution of turning angles and flight velocity for each of the movement behaviours considered was then analysed and reproduced in the ABM according to randomly generated values within specific data distributions (see 7. 'Sub-models: Foraging behaviour' for additional information).

7. Sub-models

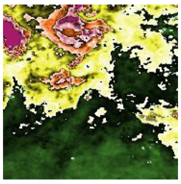
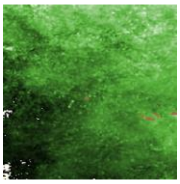
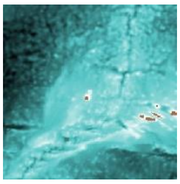
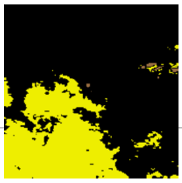
Set environmental layers (To import-world)

Environmental layers (i.e. CHA, SST and bathymetry) are imported in the form of ESRI ASCII Grid files, using the GIS extension for NetLogo (https://ccl.northwestern.edu/netlogo/docs/gis.html).

Update world's view and resources availability (To setup-world)

The world's view (Table 4) can be displayed according to different backgrounds associated with the environmental layers considered (interface: *paint-patch*). If one of the environmental layers is selected, specific colour scales and associated ranges of values are set, otherwise the background is displayed in black. Patches of land (islands from Azores archipelago) are represented in brown. Profitable sea patches are established upon specific thresholds of CHL, SST and bathymetry (BAT), which are then displayed in the world's view as yellow patches.

Table 4 - Description of the world's view characterization.

	Colour	**Patch values**	**World's view**
Islands	Brown	CHL = 0; SST = 0; BAT = 0	
Chlorophyll-a concentration	Scale-color green	]0; 0.1]	
	Scale-color yellow	]0.1; 0.15]	
	Scale-color orange	]0.15; 0.2]	
	Scale-color pink	]0.2; 0.25]	
	Scale-color magenta	]0.25; [	
Sea surface temperature	Scale-color green	[20; 25]	
	Scale-color yellow	]25; 30]	
Bathymetry	Scale-color blue	[0; 4600]	
Feeding areas	Yellow	Upon predefined environmental thresholds.	

Run the simulation (To Go)

Simulation extent

Restriction of the simulation to a limited temporal extent, and definition of the intended length for the simulation; options selection in the interface (see 5. ‘Initialization: Interface’ for additional information).

Movement tracking

Visual display of the individuals’ movement along the simulation and across the seascape; option selection in the interface (see 5. ‘Initialization: Interface’ for additional information).

Data to export

Selection of 20 random virtual birds per sub-colony to data extraction; option selection in the interface (see 5. “Initialization: Interface” for additional information). For each selected individual (with independent ID generation from 1 to 20), a “clone” is created in order to store the tracking data of the respective host individual along simulation. The data is recorded individually per tick, and subjected to extraction at the end of each simulation (see 7. ‘Sub-models: Write outputs’ for additional information).

Foraging patches’ density of use

Calculation of the density of use of each patch in the seascape, for each sub-colony separately; option selection in the interface (see 5. ‘Initialization: Interface’ for additional information). Each patch records the cumulative number of visits by virtual birds (either in travelling or ARS mode), creating a colour gradient to the number of entrances in the respective patch, with darker colours representing higher densities of patch visits. The density of use per patch is updated per tick, and each sub-colony has its own identification colour (sub-colony A in blue and sub-colony B in red).

Foraging behaviour (To move)

Virtual Cory’s shearwaters move throughout the seascape according to specific flight characteristics associated with two movement behaviours: Area Restricted Search and Travelling. Virtual birds assume a travelling mode while searching for resources (i.e. “flying” over unprofitable patches) and perform ARS whenever on profitable patches, i.e. virtual birds increase velocity and reduce turning angle as a response to decreased productivity and reduce speed and increase turning rate as a response to increased productivity in a restricted area (Figure 4).

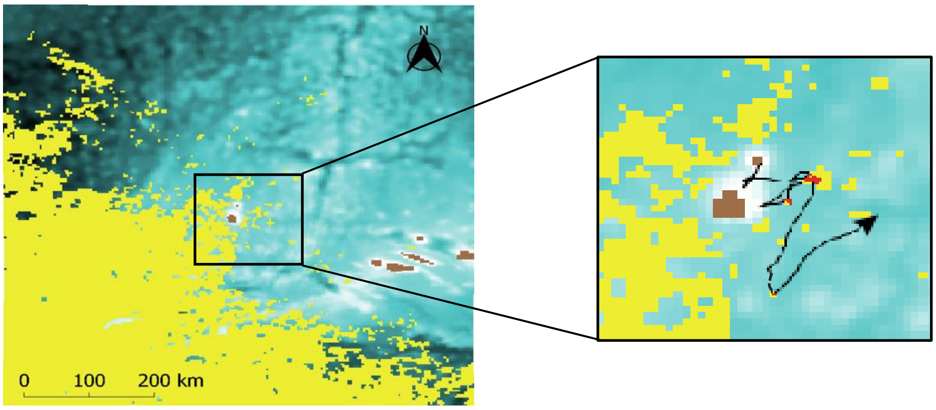


Figure 4 - Example of the movement behaviour of a virtual individual during foraging. The lines represent the movement throughout the simulation: (A) the individual performs ARS (in red) on a feeding area (in yellow), increasing the turning angle and decreasing the velocity; (B) the individual travels (in black) over unprofitable patches (in blue), decreasing the turning angle and increasing the velocity.

The probability distribution of turning angles and flight speed for travelling and ARS were based on real movement data of Cory's shearwaters, and reproduced in the ABM according to randomly generated values within specific data distributions (Figure 5):

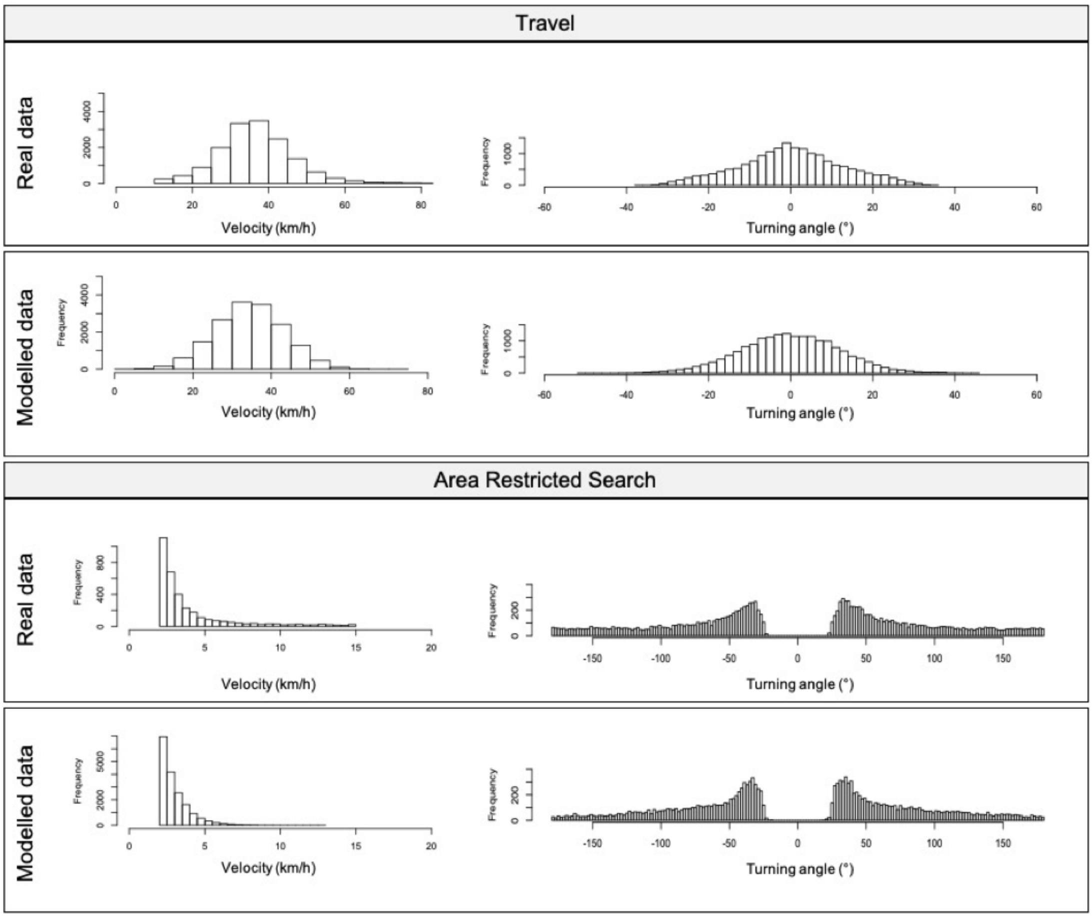


Figure 5 - Probability distribution of turning angles and flight speed for two movement behaviour, Travelling and ARS: movement data extracted from 368 local foraging trips (<1 day) of real Cory's shearwaters around the Corvo Island (Azores archipelago, Portugal) *versus* modelled data of virtual Cory's shearwaters.

Travel:

- Turning angle

```
set turn-angle random-normal 0 12
set heading heading + turn-angle
```

- Flight speed*

```
set speed-travel random-normal 0.7167 0.18125
fd speed-travel
```

ARS:

- Turning angle

```
set turn-angle ifelse-value (random-normal 0 10 > 0)
    [ 25 + random-exponential 80 ]
    [ -25 - random-exponential 80 ]
    if turn-angle > 180
    [ set turn-angle random-poisson 35 ]
```

```
    if turn-angle < -180
    [ set turn-angle 0 - random-poisson 35 ]
set heading heading + turn-angle
```

- Flight speed*

```
set speed-ars 0.04167 + random-exponential 0.02083
fd speed-ars
```

*The flight speed was scaled at the pixels dimension.

Avoid land

Virtual birds are able to sense land in the direction they are moving, rotating 180 degrees in order to avoid it.

Uninformed Search

In the Uninformed search, virtual individuals are unable to perceive external information, thus moving throughout the seascape solely relying on the information of the patch they are in (Figure 6).

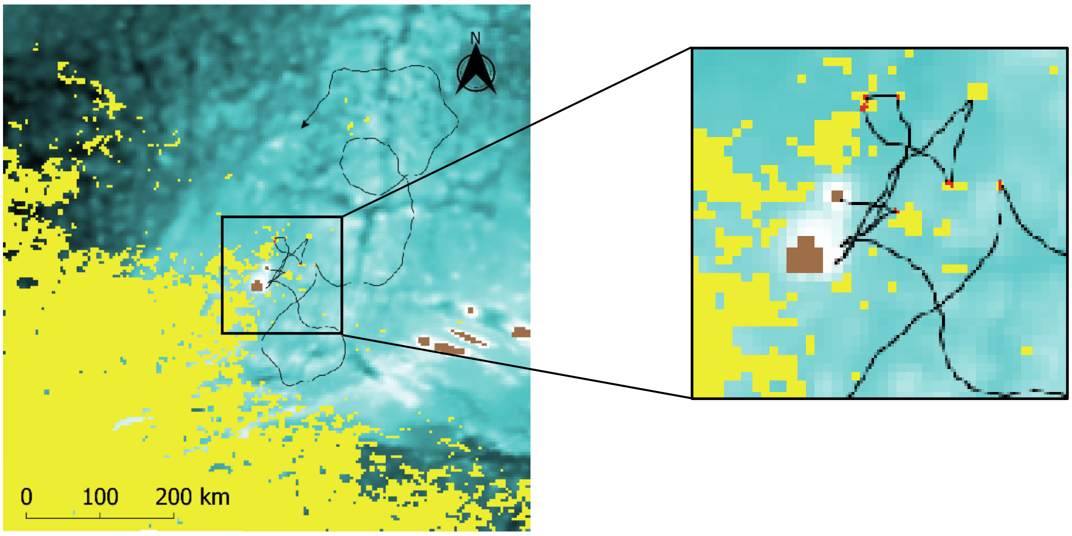


Figure 6 - Example of the movement behaviour of a virtual individual foraging according to the Uninformed search. The lines represent the movement throughout the simulation: the individual is unable to forecast profitable foraging areas thus describing an erratic search. The individual travel (in black) over unprofitable patches (in blue), and perform ARS (in red) whenever on a feeding area (in yellow).

Tracking olfactory cues

In the Olfactory search, virtual individuals can percept the characteristics of the surrounding environment (Figure 7). Yet, in order to reproduce some uncertainty in food detectability through smell, birds only have access to one patch randomly selected within their perception angle. In this way, the more profitable the areas where a virtual bird is foraging, the more likely is to detect a feeding patch. Therefore, whenever virtual birds sense a profitable area within their olfactory range (see 4.1. 'Basic Principles: Sensing' for additional information), the heading is adjusted and the travelling is biased towards the identified patch.

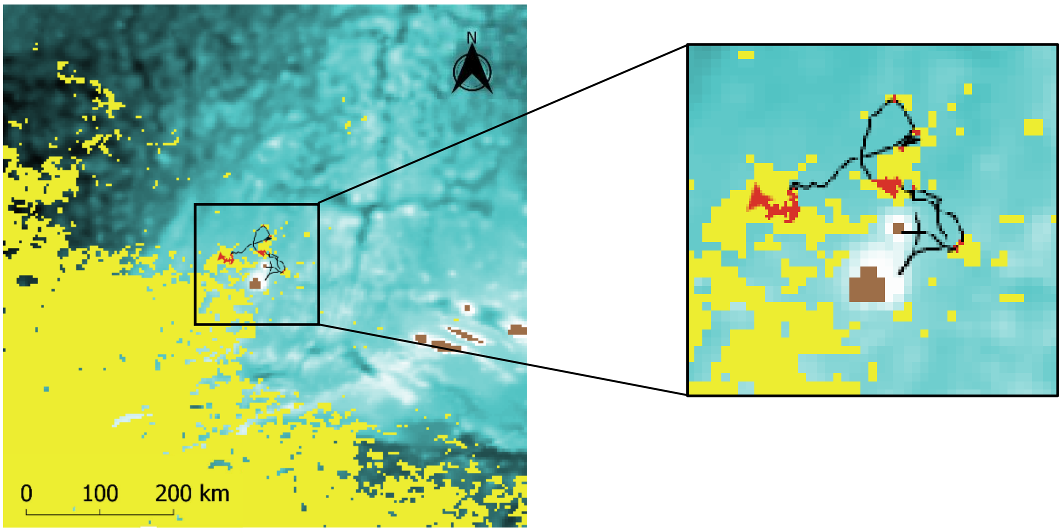


Figure 7 - Example of the movement behaviour of a virtual individual foraging according to the Olfactory search. The lines represent the movement throughout the simulation: the individual show a directed search towards profitable feeding areas (in yellow). The individual travel (in black) over unprofitable patches (in blue), whereas perform ARS (in red) whenever on a feeding area (in yellow).

Tracking social information

Virtual birds can monitor the behaviour of conspecifics (regardless the sub-colony of origin) and converge into the location where other individuals are performing Area Restricted Search (Figure 8A and 8B). In the case of visual contact with multiple feeding individuals (in the same or different patches), virtual birds choose the closest individual. Therefore, whenever they percept a foraging patch location through visual contact with other birds (see 4.1. 'Basic Principles: Sensing' for additional information), the turning angle is updated triggering a biased traveling towards the newly identified feeding area (Figure 8A and 8B).

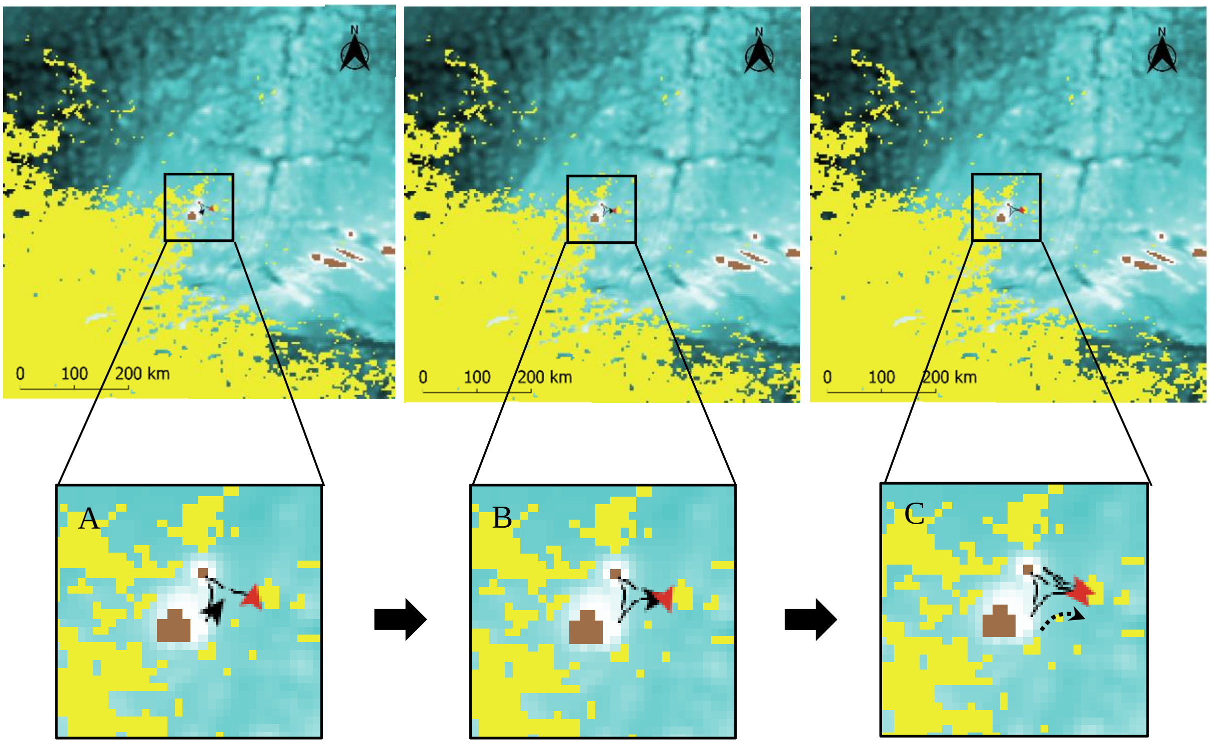


Figure 8 - Example of the movement behaviour of virtual individuals using local enhancement (A and B) and foraging according to the olfactory search with local enhancement (C): (A) individual 1 (in black) detects within its visual angle the individual 2 performing ARS (in red); (B) individual 1 (in black) adjusts travelling towards the individual 2 (in red); (C) individual 1 reaches the feeding area performing ARS together with individual 2 (in red); another individual (dotted line) is searching nearby but not detects the conspecifics thus following its travel trajectory.

Tracking olfactory cues and social information

Virtual birds can continuously scan the landscape using olfactory or social cues to identify profitable patches. Therefore, if only olfactory or social information is available, the travelling is biased towards the patch identified by solely one of the mechanisms (Figure 7 and Figure 8A and 8B). However, when either olfactory and social information are simultaneously available, both are involved in the individuals movement behaviour (Figure 8C). In particular, if a patch is visually identified, individuals head in line with social information first, yet they still consider olfactory cues before deciding where to move. Consequently, if they also find a profitable patch based on olfactory cues, the heading is readjusted and the travelling is biased towards the patch recognised through smell (Figure 8C). In this way, both cues are always involved in the individuals foraging decision and simultaneously contribute to increase the probability of individuals to find a profitable feeding patch.

Feeding behaviour (To feed)

Virtual birds gain 1 unit of energy for each time step (i.e. 5 minutes) spent on a feeding patch. The energy is updated as soon as its value is calculated by the respective process (asynchronous updating) and the cumulative energy obtained by each individual is updated throughout the simulation (i.e. energy score).

Write outputs (To export)

Exportation of tracking data from a sub-sample of virtual individuals (see 7. ‘Submodels: Run the simulation’ for additional information), by creating a GIS file (.shp) per sub-colony, through the GIS extension for NetLogo (https://ccl.northwestern.edu/netlogo/docs/gis.html); option selection in the interface (see 5. “Initialization: Interface” for additional information).

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Appendix E

According to Lee et al. (2015) the purpose of a sensitivity analysis is to provide a measure of the robustness of the model, measuring the sensitivity of the obtained results to changes in parameters, forcing functions and/or sub-models. Global Sensitivity Analysis, measuring the effect of combined parameters of a model in terms of sensitivity, was performed by estimating standardized regression coefficients (SRC) associated to a matrix of combinations of the parameters with +/−10% variation of the respective values (Lee et al. 2015). SRC expresses the magnitude and significance of the effect of combined parameters measured using different units, as well as the explained variance, gauging the main effects of the input parameters. A stepwise multiple regression analysis (based on Generalized Linear Models) was used to test for relationships between the energy score of individuals from sub-colony A and parameters of movement behaviour (speed and turning angle of ARS and travelling), visual and olfactory acuity (visual acuity and perception angles of olfactory and visual stimuli), and the initial heading at departure from the colony. The sensitivity of the model was tested in the scenario of intermediate foraging conditions and the variation of the parameters was evaluated for each foraging strategy, considering 1 replicate of 100 individuals, 10 replicates of 10 individuals and 100 replicates of 1 individual. All simulations were then combined into a single database and a stepwise procedure (both directions) was applied so that the effect of each parameter could be added or removed in order to find the model with the smallest Akaike Information Criterion (Hastie and Pregibon 1992; Venables and Ripley 2002). This allowed to discriminate the magnitude and significance of the effect that each parameter caused in variations of energy gains after a foraging day. The lack of substantial intercorrelation among parameters was confirmed by the inspection of the respective Spearman's rho correlation coefficient lower than 0.7 (Elith et al. 2006). Since the response variable (energy score of individuals from sub-colony A after a foraging day) assumed an exponential distribution, a Gamma variance distribution with a Negative inverse link function was used to run Generalized Linear Models. The statistical analysis was carried out using the *glm* and *step* functions in the stats R package (R Development Core Team 2017). Results from the SRC sensitivity analyses indicate that speed of ARS and of travelling, visual acuity and the perception angles of olfactory and of visual stimuli were key parameters that caused the main variations in the individuals' energy gains after a foraging day (Table 1). On contrary, the turning angle of ARS and of travelling, and the initial heading at departure from the colony didn't have a significant influence in the response. Nevertheless, all surviving parameters to the stepwise procedure (ARS angle, Travelling speed, Olfactory distance and the Initial heading at departure from the colony) can be considered with influence on the model outcomes (Table 1).

Table 1 – Generalized linear model outputs for the influence of movement behaviour (speed and turning angle of ARS and travelling), visual and olfactory acuity (visual acuity and perception angles of olfactory and visual stimuli), and the initial heading at departure from the colony in the energy score of individuals from sub-colony A (Null deviance: 117832 on 808206 degrees of freedom; Residual deviance: 117561 on 808197 degrees of freedom; AIC: 7963668): +/−10% variation of the variables' values (Sensitivity), variable coefficient (Estimate), variable standard error (Std. Error), variable z-value (z value), and variable significance (Pr(>|z|)). Significant variables are signed in bold.

Variable	Sensitivity			Estimate	Std. Error	z value	Pr(>|z|)
	-10%	0	10%				
Initial heading colony A	40.5	45	49.5	2.394e-06	3.251e-06	0.737	0.46136
ARS angle	22.5	25	27.5	7.046e-06	5.860e-06	1.202	0.22926
Travelling angle	-1.2	0	1.2	1.976e-05	1.220e-05	1.620	0.10519
ARS speed	**0.037**	**0.042**	**0.046**	**2.722e-02**	**3.517e-03**	**7.741**	**9.84e-15**
Travelling speed	**0.645**	**0.717**	**0.788**	**-2.725e-03**	**2.045e-04 -**	**-13.327**	**< 2e-16**
Vision distance	**2.25**	**2.5**	**2.75**	**2.079e-04**	**7.225e-05**	**2.878**	**0.00401**
Vision angle	**133.2**	**148**	**162.8**	**3.536e-06**	**1.221e-06**	**2.897**	**0.00377**
Olfactory distance	4.5	5	5.5	-5.242e-05	3.513e-05	-1.492	0.13563
Olfactory angle	**162**	**180**	**198**	**-3.245e-06**	**1.004e-06**	**-3.232**	**0.00123**

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Appendix F - Results from the two-way Scheirer-Ray-Hare test for the influence of foraging conditions (FC) and the foraging mechanisms (with the number of individuals nested) (FM (NI)), including interaction term (FC x FM(NI)), in the energy obtained by virtual individuals after a foraging day (median of energy score): Degrees of freedom (Df), sum of squares (SS), chi-squared (χ^2) and respective significance (p-value).

Factors	**Df**	**SS**	**χ^2 (p-value)**
FC	2	6890984595	3648.6 (0.000)
FM (NI)	15	546592447	289.4 (0.000)
FC x FM (NI)	30	380970729	201.7 (0.000)
Residuals	4725	1245101215	

Appendix G - Results from the Steel-Dwass-Critchlow-Fligner multiple-comparisons test and statistical significance (p-value) for each comparison (upper side); Absolute differences in energy (median of energy score) for each comparison (lower side).

			GOOD FORAGING CONDITIONS																BASELINE FORAGING CONDITIONS																POOR FORAGING CONDITIONS															
			US				OS				LE				OSLE				US				OS				LE				OSLE				US				OS				LE				OSLE			
			1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1	1000	100	10	1
GOOD FORAGING CONDITIONS	US	1000		-1.321 (1.0000)	-17.097 (< 2.22e-16	-1.387 (1.0000)	-17.749 (< 2.22e-16)	-17.496 (< 2.22e-16)	-17.266 (< 2.22e-16)	-10.566 (8.9746e-11	-17.533 (< 2.22e-16	-17.364 (< 2.22e-16)	-12.451 (3.6982e-13	-0.446 (1.0000)	-17.661 (< 2.22e-16	-17.607 (< 2.22e-16)	-17.263 (< 2.22e-16)	-12.633 (3.4039e-13	-17.501 (< 2.22e-16)	-17.395 (< 2.22e-16)	-14.363 (4.5364e-13	-6.549 (0.0034)	-9.294 (5.5745e-08)	-5.827 (0.0291)	-3.834 (0.8349)	-0.255 (1.0000)	-17.097 (< 2.22e-16)	-4.819 (0.2762)	-11.734 (6.3793e-13	-8.516 (1.9147e-06)	18.055 (< 2.22e-16)	-15.663 (2.3448e-13)	-3.120 (0.9913)	-1.007 (1.0000)	-18.607 (< 2.22e-16)	-18.567 (< 2.22e-16	-17.576 (< 2.22e-16)	-17.597 (< 2.22e-16)	-18.607 (< 2.22e-16)	-18.221 (< 2.22e-16)	-17.472 (< 2.22e-16)	-17.597 (< 2.22e-16)	-18.567 (< 2.22e-16)	-18.349 (< 2.22e-16)	-17.873 (< 2.22e-16)	-17.658 (< 2.22e-16)	-18.316 (< 2.22e-16)	-17.797 (< 2.22e-16)	-17.597 (< 2.22e-16)	-17.597 (< 2.22e-16)
		100	1		-3.618 (0.9149)	-1.215 (1.0000)	-17.647 (< 2.22e-16)	-17.384 (< 2.22e-16)	-16.951 (< 2.22e-16)	-10.368 (2.5780e-10	17.406 (< 2.22e-16)	-17.051 (< 2.22e-16)	-11.197 (3.4002e-12	-0.673 (1.0000)	17.560 (< 2.22e-16	-17.507 (< 2.22e-16)	-16.948 (< 2.22e-16)	-12.564 (3.4628e-13)	-17.396 (< 2.22e-16)	-17.061 (< 2.22e-16)	-13.848 (5.0671e-13	-6.609 (0.0028)	-6.297 (0.0076)	-4.832 (0.2703)	-3.678 (0.8961)	-0.159 (1.0000)	-16.045 (< 2.22e-16)	-2.203 (0.9999)	-11.233 (2.8845e-12	-8.352 (3.8867e-06)	17.260 (< 2.22e-16)	-13.663 (3.4561e-13)	-1.939 (0.9999)	-1.244 (1.0000)	-18.489 (< 2.22e-16)	-18.450 (< 2.22e-16)	-17.476 (< 2.22e-16)	-17.497 (< 2.22e-16)	-18.489 (< 2.22e-16)	-18.110 (< 2.22e-16)	-17.374 (< 2.22e-16)	17.497 (< 2.22e-16)	-18.450 (< 2.22e-16)	-18.235 (< 2.22e-16)	-17.768 (< 2.22e-16)	-17.556 (< 2.22e-16)	-18.203 (< 2.22e-16)	-17.694 (< 2.22e-16)	-17.497 (< 2.22e-16)	-17.497 (< 2.22e-16)
		10	1	2		-2.325 (0.9999)	-17.078 (< 2.22e-16)	-16.781 (< 2.22e-16)	-15.913 (8.5265e-14	-10.727 (3.7741e-11	16.982 (< 2.22e-16)	-15.540 (3.7303e-13)	-10.630 (6.3775e-11	-2.488 (0.9999)	17.511 (< 2.22e-16	-17.388 (< 2.22e-16)	-16.116 (< 2.22e-16)	-13.054 (5.3124e-13)	-11.444 (1.2595e-12	-10.797 (2.5747e-11)	-9.428 (2.9390e-08)	-4.775 (0.2974)	-1.844 (0.9999)	-2.080 (0.9999)	-1.077 (1.0000)	-2.135 (0.9999)	11.991 (4.8939e-13	-4.546 (0.4225)	-5.772 (0.0337)	-6.352 (0.0064)	14.143 (3.7703e-13	-10.025 (1.5212e-09)	-3.920 (0.7945)	-0.173 (1.0000)	-18.472 (< 2.22e-16)	-18.433 (< 2.22e-16)	-17.462 (< 2.22e-16)	-17.320 (< 2.22e-16	-18.472 (< 2.22e-16)	-18.095 (< 2.22e-16)	-17.360 (< 2.22e-16)	-17.439 (< 2.22e-16)	-18.433 (< 2.22e-16)	-18.219 (< 2.22e-16)	-17.754 (< 2.22e-16)	-17.490 (< 2.22e-16)	-18.187 (< 2.22e-16)	-17.679 (< 2.22e-16)	-17.483 (< 2.22e-16)	-17.294 (< 2.22e-16)
		1	2	1	3		-5.257 (0.1172)	-5.237 (0.1224)	-5.489 (0.0689)	-4.438 (0.4878)	-5.972 (0.0195)	-4.315 (0.5645)	-2.228 (0.9999)	-0.605 (1.0000)	-7.558 (9.6824e-05)	-7.012 (0.0007)	-5.826 (0.0292)	-5.595 (0.0531)	-5.728 (0.0378)	-5.729 (0.0377)	-6.325 (0.0069)	-5.455 (0.0746)	-2.363 (0.9999)	-2.101 (0.9999)	-2.056 (0.9999)	-1.271 (1.0000)	-1.895 (0.9999)	-0.826 (1.0000)	-4.387 (0.5199)	-6.730 (0.0019)	-3.020 (0.9953)	-1.296 (1.0000)	-0.780 (1.0000)	-2.546 (0.9999)	-18.474 (< 2.22e-16)	-18.435 (< 2.22e-16)	-17.460 (< 2.22e-16)	-16.678 (< 2.22e-16)	-18.474 (< 2.22e-16)	-18.096 (< 2.22e-16)	-17.329 (< 2.22e-16)	-16.872 (< 2.22e-16)	-18.435 (< 2.22e-16)	-18.221 (< 2.22e-16)	-17.748 (< 2.22e-16)	-16.891 (< 2.22e-16)	-18.188 (< 2.22e-16)	-17.681 (< 2.22e-16)	-17.440 (< 2.22e-16)	-16.475 (< 2.22e-16)
	OS	1000	8	7	9	6		-0.004 (1.0000)	-0.679 (1.0000)	-0.496 (1.0000)	-7.144 (0.0005)	-9.938 (2.3753e-09)	-13.444 (3.9801e-13	-8.943 (2.8537e-07)	16.508 (< 2.22e-16	-14.676 (4.2544e-13)	-3.981 (0.7630)	-3.083 (0.9931)	-17.747 (< 2.22e-16)	-17.636 (< 2.22e-16)	-17.632 (< 2.22e-16)	-13.872 (4.9738e-13)	-18.024 (< 2.22e-16)	17.660 (< 2.22e-16)	-17.634 (< 2.22e-16)	-12.980 (5.6277e-13	-18.042 (< 2.22e-16)	-17.659 (< 2.22e-16)	-17.170 (< 2.22e-16)	-15.809 (1.2790e-13)	18.470 (< 2.22e-16)	-17.713 (< 2.22e-16)	-17.263 (< 2.22e-16)	-13.695 (5.8709e-13)	-18.903 (< 2.22e-16)	-18.862 (< 2.22e-16)	-17.825 (< 2.22e-16)	-17.847 (< 2.22e-16)	-18.903 (< 2.22e-16)	-18.500 (< 2.22e-16)	-17.717 (< 2.22e-16)	-17.847 (< 2.22e-16)	-18.862 (< 2.22e-16)	-18.633 (< 2.22e-16)	-18.135 (< 2.22e-16)	-17.910 (< 2.22e-16)	-18.598 (< 2.22e-16)	-18.056 (< 2.22e-16)	-17.847 (< 2.22e-16)	-17.847 (< 2.22e-16)
		100	8	7	9	6	0		-0.620 (1.0000)	538 (1.0000)	-6.342 (0.0066)	-9.182 (9.4687e-08)	-12.972 (5.6977e-13	-8.800 (5.4677e-07)	15.411 (4.6652e-13	-13.469 (3.9024e-13)	-3.581 (0.9252)	-2.870 (0.9984)	-17.494 (< 2.22e-16)	-17.388 (< 2.22e-16)	-17.383 (< 2.22e-16	-13.612 (3.5416e-13)	-17.759 (< 2.22e-16)	17.410 (< 2.22e-16)	-17.379 (< 2.22e-16)	-12.730 (3.1652e-13)	-17.770 (< 2.22e-16)	-17.410 (< 2.22e-16)	-16.920 (< 2.22e-16)	-15.518 (4.1567e-13)	18.108 (< 2.22e-16)	-17.455 (< 2.22e-16)	-16.937 (< 2.22e-16)	-13.448 (4.0223e-13	-18.598 (< 2.22e-16)	-18.558 (< 2.22e-16)	-17.568 (< 2.22e-16)	-17.589 (< 2.22e-16)	-18.598 (< 2.22e-16)	-18.213 (< 2.22e-16)	-17.465 (< 2.22e-16)	-17.589 (< 2.22e-16)	-18.558 (< 2.22e-16)	-18.340 (< 2.22e-16)	-17.865 (< 2.22e-16)	-17.650 (< 2.22e-16)	-18.307 (< 2.22e-16)	-17.790 (< 2.22e-16)	-17.589 (< 2.22e-16)	-17.589 (< 2.22e-16)
		10	7.5	6.5	8.5	5.5	0.5	0.5		-0.660 (1.0000)	-3.898 (0.8053)	-5.586 (0.0543)	-10.825 (2.2208e-11	-8.713 (8.0722e-07)	-9.976 (1.9581e-09)	-8.372 (3.5655e-06)	-2.241 (0.9999)	-1.910 (0.9999)	-17.396 (< 2.22e-16)	-17.291 (< 2.22e-16)	-17.246 (< 2.22e-16	-13.063 (5.2913e-13	-17.655 (< 2.22e-16)	17.298 (< 2.22e-16)	-16.829 (< 2.22e-16)	-11.933 (5.0804e-13)	15.682 (2.1316e-13	17.079 (< 2.22e-16)	-16.728 (< 2.22e-16)	-14.796 (4.5741e-13)	14.288 (5.0249e-13	-15.993 (6.3949e-14)	-15.622 (2.7711e-13)	-12.860 (6.1562e-13)	-18.481 (< 2.22e-16)	-18.442 (< 2.22e-16)	-17.469 (< 2.22e-16)	-17.490 (< 2.22e-16)	-18.481 (< 2.22e-16)	-18.103 (< 2.22e-16)	-17.367 (< 2.22e-16)	-17.490 (< 2.22e-16)	-18.442 (< 2.22e-16)	-18.227 (< 2.22e-16)	-17.761 (< 2.22e-16)	-17.550 (< 2.22e-16)	-18.195 (< 2.22e-16)	-17.687 (< 2.22e-16)	-17.490 (< 2.22e-16)	-17.490 (< 2.22e-16)
		1	7.5	6.5	8.5	5.5	0.5	0.5	0		-1.901 (0.9999)	-1.957 (0.9999)	-5.530 (0.0624)	-6.430 (0.0050)	-4.946 (0.2202)	-3.963 (0.7725)	-1.421 (1.0000)	-1.641 (1.0000)	-13.926 (4.7073e-13	-13.872 (4.9516e-13)	-13.922 (4.7118e-13	-10.948 (1.1337e-11)	-11.277 (2.3731e-12)	10.957 (1.0836e-11	-10.902 (1.4604e-11)	-8.268 (5.5396e-06)	-7.655 (6.6630e-05)	10.215 (5.7326e-10)	-12.583 (3.4861e-13	-12.225 (4.1933e-13)	-6.460 (0.00456)	-8.280 (5.2750e-06)	-9.599 (1.2832e-08)	-9.524 (1.8474e-08)	-18.480 (< 2.22e-16)	-18.441 (< 2.22e-16)	-17.469 (< 2.22e-16)	-17.365 (< 2.22e-16)	-18.480 (< 2.22e-16)	-18.102 (< 2.22e-16)	-17.367 (< 2.22e-16)	-17.453 (< 2.22e-16)	-18.441 (< 2.22e-16)	-18.227 (< 2.22e-16)	-17.761 (< 2.22e-16)	-17.502 (< 2.22e-16)	-18.195 (< 2.22e-16)	17.686 (< 2.22e-16)	-17.490 (< 2.22e-16)	-17.358 (< 2.22e-16)
	LE	1000	8	7	9	6	0	0	0.5	0.5		-11.776 (6.0418e-13)	-13.795 (5.3535e-13	-10.059 (1.2799e-09)	10.910 (1.3964e-11	-8.039 (1.4347e-05)	-0.101 (1.0000)	-1.057 (1.0000)	-17.531 (< 2.22e-16)	-17.424 (< 2.22e-16)	-17.419 (< 2.22e-16)	-14.141 (3.7581e-13)	-17.798 (< 2.22e-16)	17.447 (< 2.22e-16)	-17.408 (< 2.22e-16)	-13.244 (4.5974e-13)	-17.801 (< 2.22e-16)	-17.446 (< 2.22e-16)	-17.033 (< 2.22e-16)	-15.743 (1.7053e-13)	18.073 (< 2.22e-16)	-17.485 (< 2.22e-16)	-17.110 (< 2.22e-16)	-14.259 (5.1970e-13)	-18.643 (< 2.22e-16)	-18.602 (< 2.22e-16)	-17.606 (< 2.22e-16)	-17.627 (< 2.22e-16)	-18.643 (< 2.22e-16)	-18.255 (< 2.22e-16)	-17.502 (< 2.22e-16)	-17.627 (< 2.22e-16)	-18.602 (< 2.22e-16)	-18.383 (< 2.22e-16)	-17.905 (< 2.22e-16)	-17.688 (< 2.22e-16)	-18.350 (< 2.22e-16)	-17.828 (< 2.22e-16)	-17.627 (< 2.22e-16)	-17.627 (< 2.22e-16)
		100	7	6	8	5	1	1	0.5	0.5	1		-8.705 (8.3629e-07)	-7.130 (0.0005)	16.392 (< 2.22e-16	15.499 (4.4764e-13)	-8.067 (1.2806e-05)	-5.040 (0.1839)	-17.429 (< 2.22e-16)	-17.324 (< 2.22e-16)	-17.299 (< 2.22e-16)	-12.042 (4.7240e-13	-17.691 (< 2.22e-16)	17.346 (< 2.22e-16)	-16.926 (< 2.22e-16)	-10.871 (1.7302e-11)	-16.285 (< 2.22e-16)	17.238 (< 2.22e-16)	-16.664 (< 2.22e-16)	14.218 (5.4901e-13)	13.781 (5.4090e-13	-16.598 (< 2.22e-16)	-15.316 (4.6396e-13)	-11.620 (7.8326e-13)	-18.520 (< 2.22e-16)	-18.481 (< 2.22e-16)	-17.502 (< 2.22e-16)	-17.523 (< 2.22e-16)	-18.520 (< 2.22e-16)	-18.140 (< 2.22e-16)	-17.400 (< 2.22e-16)	-17.523 (< 2.22e-16)	-18.481 (< 2.22e-16)	-18.265 (< 2.22e-16)	-17.796 (< 2.22e-16)	-17.583 (< 2.22e-16)	-18.233 (< 2.22e-16)	-17.721 (< 2.22e-16)	-17.523 (< 2.22e-16)	-17.523 (< 2.22e-16)
		10	4.75	3.75	5.75	2.75	3.25	3.25	2.75	2.75	3.25	2.25		-4.029 (0.7369)	15.717 (1.8119e-13	15.291 (4.2188e-13)	11.651 (7.4318e-13)	-7.983 (1.8068e-05)	-17.391 (< 2.22e-16)	-17.048 (< 2.22e-16)	-15.992 (6.3949e-14	-9.656 (9.6873e-09)	-14.454 (4.0490e-13	13.560 (3.7026e-13	-11.948 (5.0271e-13)	-6.355 (0.0063)	-2.244 (0.9999)	-10.975 (9.7881e-12	14.473 (3.9824e-13	-11.518 (1.0107e-12)	-1.580 (1.0000)	-4.478 (0.4633)	-8.226 (6.6091e-06)	-7.310 (0.0003)	-18.475 (< 2.22e-16)	-18.436 (< 2.22e-16)	-17.464 (< 2.22e-16)	-17.485 (< 2.22e-16)	-18.475 (< 2.22e-16)	-18.097 (< 2.22e-16)	-17.363 (< 2.22e-16)	-17.485 (< 2.22e-16)	-18.436 (< 2.22e-16)	-18.222 (< 2.22e-16)	-17.756 (< 2.22e-16)	-17.545 (< 2.22e-16)	-18.190 (< 2.22e-16)	-17.682 (< 2.22e-16)	-17.485 (< 2.22e-16)	-17.485 (< 2.22e-16)
		1	1.5	0.5	2.5	0.5	6.5	6.5	6	6	6.5	5.5	3.25		-12.045 (4.6230e-13	-11.525 (9.8899e-13)	-9.394 (3.4706e-08)	-8.173 (8.2627e-06)	-8.642 (1.1054e-06)	-8.168 (8.4459e-06)	-7.871 (2.8372e-05)	-5.668 (0.0441)	-1.274 (1.0000)	-1.404 (1.0000)	-1.897 (0.9999)	-0.832 (1.0000)	-4.014 (0.7449)	-0.149 (1.0000)	-5.571 (0.0564)	-7.044 (0.0006)	-5.563 (0.0575)	2.863 (0.9984)	-0.278 (1.0000)	-2.324 (0.9999)	-18.474 (< 2.22e-16)	-18.433 (< 2.22e-16)	-17.300 (< 2.22e-16)	-16.792 (< 2.22e-16)	-18.474 (< 2.22e-16)	-18.073 (< 2.22e-16)	-17.140 (< 2.22e-16)	16.962 (< 2.22e-16)	-18.435 (< 2.22e-16)	-18.201 (< 2.22e-16)	-17.658 (< 2.22e-16)	-17.055 (< 2.22e-16)	-18.174 (< 2.22e-16)	-17.596 (< 2.22e-16)	-17.303 (< 2.22e-16)	-16.715 (< 2.22e-16)
	OSLE	1000	9	8	10	7	1	1	1.5	1.5	1	2	4.25	7.5		-4.026 (0.7383)	-7.733 (4.9007e-05)	-2.972 (0.9966)	-17.659 (< 2.22e-16)	-17.550 (< 2.22e-16)	-17.545 (< 2.22e-16	-15.249 (4.6629e-13	-17.932 (< 2.22e-16)	17.573 (< 2.22e-16)	-17.548 (< 2.22e-16)	-14.385 (4.4531e-13	-17.950 (< 2.22e-16)	17.572 (< 2.22e-16)	-17.300 (< 2.22e-16)	-16.350 (< 2.22e-16)	18.371 (< 2.22e-16)	-17.626 (< 2.22e-16)	-17.531 (< 2.22e-16)	-15.825 (1.1724e-13)	-18.797 (< 2.22e-16)	-18.756 (< 2.22e-16)	-17.735 (< 2.22e-16)	-17.757 (< 2.22e-16)	-18.797 (< 2.22e-16)	-18.400 (< 2.22e-16)	-17.629 (< 2.22e-16)	-17.757 (< 2.22e-16)	-18.756 (< 2.22e-16)	-18.531 (< 2.22e-16)	-18.041 (< 2.22e-16)	-17.820 (< 2.22e-16)	-18.497 (< 2.22e-16)	-17.963 (< 2.22e-16)	-17.757 (< 2.22e-16)	-17.757 (< 2.22e-16)
		100	9	8	10	7	1	1	1.5	1.5	1	2	4.25	7.5	0		-5.365 (0.0921)	-1.581 (1.0000)	-17.605 (< 2.22e-16)	-17.497 (< 2.22e-16)	-17.492 (< 2.22e-16	-14.943 (4.7329e-13	-17.875 (< 2.22e-16)	17.520 (< 2.22e-16)	-17.495 (< 2.22e-16)	-14.073 (4.0756e-13	-17.893 (< 2.22e-16)	17.519 (< 2.22e-16)	-17.193 (< 2.22e-16)	-16.202 (< 2.22e-16)	18.310 (< 2.22e-16)	-17.572 (< 2.22e-16)	-17.435 (< 2.22e-16)	-15.397 (4.8639e-13)	-18.732 (< 2.22e-16)	-18.691 (< 2.22e-16)	-17.681 (< 2.22e-16)	-17.702 (< 2.22e-16)	-18.732 (< 2.22e-16)	-18.339 (< 2.22e-16)	-17.575 (< 2.22e-16)	-17.702 (< 2.22e-16)	-18.691 (< 2.22e-16)	-18.468 (< 2.22e-16)	-17.984 (< 2.22e-16)	-17.764 (< 2.22e-16)	-18.435 (< 2.22e-16)	-17.906 (< 2.22e-16)	-17.702 (< 2.22e-16)	-17.702 (< 2.22e-16)
		10	8.25	7.25	9.25	6.25	0.25	0.25	0.75	0.75	0.25	1.25	3.5	6.75	0.75	0.75		-1.014 (1.000)	-17.402 (< 2.22e-16)	-17.297 (< 2.22e-16)	-17.239 (< 2.22e-16)	-13.473 (3.9635e-13)	-17.661 (< 2.22e-16)	17.302 (< 2.22e-16)	-16.827 (< 2.22e-16)	-12.358 (3.9146e-13	15.338 (4.3421e-13	-17.075 (< 2.22e-16)	16.766 (< 2.22e-16)	-15.035 (4.7995e-13)	14.404 (4.3121e-13	-15.765 (1.4921e-13)	-15.810 (1.2790e-13)	-13.379 (4.2000e-13)	-18.487 (< 2.22e-16)	-18.448 (< 2.22e-16)	-17.475 (< 2.22e-16)	-17.495 (< 2.22e-16)	-18.487 (< 2.22e-16)	-18.109 (< 2.22e-16)	-17.373 (< 2.22e-16)	-17.495 (< 2.22e-16)	-18.448 (< 2.22e-16)	-18.234 (< 2.22e-16)	-17.767 (< 2.22e-16)	-17.555 (< 2.22e-16)	-18.201 (< 2.22e-16)	-17.692 (< 2.22e-16)	-17.495 (< 2.22e-16)	-17.495 (< 2.22e-16)
		1	9	8	10	7	1	1	1.5	1.5	1	2	4.25	7.5	0	0	0.75		-16.363 (< 2.22e-16)	-16.218 (< 2.22e-16)	15.702 (2.0250e-13	-12.406 (3.7614e-13)	13.424 (4.0368e-13	13.123 (5.1048e-13	-13.167 (4.9272e-13)	-10.178 (6.9477e-10	-9.814 (4.4188e-09)	12.304 (3.9457e-13	14.804 (4.4809e-13	13.621 (3.4928e-13)	8.573 (1.4931e-06)	-10.466 (1.5297e-10)	-11.867 (5.4767e-13)	-11.413 (1.3972e-12	-18.487 (< 2.22e-16)	-18.448 (< 2.22e-16)	-17.475 (< 2.22e-16)	-17.460 (< 2.22e-16)	-18.487 (< 2.22e-16)	-18.109 (< 2.22e-16)	-17.373 (< 2.22e-16)	-17.488 (< 2.22e-16)	-18.448 (< 2.22e-16)	-18.234 (< 2.22e-16)	-17.767 (< 2.22e-16)	-17.543 (< 2.22e-16)	-18.201 (< 2.22e-16)	-17.692 (< 2.22e-16)	-17.495 (< 2.22e-16)	-17.457 (< 2.22e-16)
BASELINE FORAGING CONDITIONS	US	1000	7	8	6	9	15	15	14.5	14.5	15	14	11.75	8.5	16	16	15.25	16		-17.396 (< 2.22e-16)	-1.958 (0.9999)	-0.396 (1.0000)	-17.765 (< 2.22e-16)	17.416 (< 2.22e-16)	-14.803 (4.5330e-13)	-9.232 (7.4917e-08)	-17.782 (< 2.22e-16)	-17.415 (< 2.22e-16)	-6.353 (0.0064)	-1.311 (1.0000)	18.191 (< 2.22e-16)	-17.467 (< 2.22e-16)	-14.808 (4.4209e-13)	-6.537 (0.0036)	-18.605 (< 2.22e-16)	-18.565 (< 2.22e-16)	-17.574 (< 2.22e-16)	-17.446 (< 2.22e-16)	-18.605 (< 2.22e-16)	-18.219 (< 2.22e-16)	-17.470 (< 2.22e-16)	-17.595 (< 2.22e-16)	-18.565 (< 2.22e-16)	-18.347 (< 2.22e-16)	-17.871 (< 2.22e-16)	-17.656 (< 2.22e-16)	-18.314 (< 2.22e-16)	-17.795 (< 2.22e-16)	-17.595 (< 2.22e-16)	-17.191 (< 2.22e-16)
		100	7	8	6	9	15	15	14.5	14.5	15	14	11.75	8.5	16	16	15.25	16	0		-1.976 (0.9999)	-0.173 (1.0000)	-17.653 (< 2.22e-16)	17.288 (< 2.22e-16)	-14.227 (5.4390e-13)	-9.042 (1.8112e-07)	-17.670 (< 2.22e-16)	-17.265 (< 2.22e-16)	-5.515 (0.0647)	-1.518 (1.0000)	18.072 (< 2.22e-16)	-17.361 (< 2.22e-16)	-14.047 (4.1811e-13)	-6.205 (0.0099)	-18.477 (< 2.22e-16)	-18.438 (< 2.22e-16)	-17.466 (< 2.22e-16)	-17.199 (< 2.22e-16)	-18.477 (< 2.22e-16)	-18.099 (< 2.22e-16)	-17.364 (< 2.22e-16)	-17.479 (< 2.22e-16)	-18.438 (< 2.22e-16)	-18.224 (< 2.22e-16)	-17.758 (< 2.22e-16)	-17.516 (< 2.22e-16)	-18.191 (< 2.22e-16)	-17.683 (< 2.22e-16)	-17.487 (< 2.22e-16)	-17.125 (< 2.22e-16)
		10	8.5	9.5	7.5	10.5	16.5	16.5	16	16	16.5	15.5	13.25	10	17.5	17.5	16.75	17.5	1.5	1.5		-0.384 (1.0000)	13.543 (3.6959e-13	13.233 (4.6729e-13	-11.622 (7.8115e-13)	-8.810 (5.2327e-07)	-17.375 (< 2.22e-16)	14.719 (4.0146e-13	-5.159 (0.1445)	-1.220 (1.0000)	18.063 (< 2.22e-16)	-16.737 (< 2.22e-16)	-12.673 (3.3251e-13)	-6.241 (0.0089)	-18.471 (< 2.22e-16)	-18.432 (< 2.22e-16)	-17.461 (< 2.22e-16)	-16.802 (< 2.22e-16)	-18.471 (< 2.22e-16)	-18.094 (< 2.22e-16)	-17.360 (< 2.22e-16)	-17.260 (< 2.22e-16)	-18.432 (< 2.22e-16)	-18.219 (< 2.22e-16)	-17.753 (< 2.22e-16)	-17.279 (< 2.22e-16)	-18.186 (< 2.22e-16)	-17.679 (< 2.22e-16)	-17.482 (< 2.22e-16)	-16.741 (< 2.22e-16)
		1	6.5	7.5	5.5	8.5	14.5	14.5	14	14	14.5	13.5	11.25	8	15.5	15.5	14.75	15.5	0.5	0.5	2		-5.831 (0.0288)	-5.919 (0.0226)	-5.430 (0.0793)	-5.409 (0.0832)	-8.992 (2.2793e-07)	-6.962 (0.0009)	-2.304 (0.9999)	-1.429 (1.0000)	10.315 (3.3913e-10	-8.426 (2.8283e-06)	-6.498 (0.0040)	-3.960 (0.7740)	-18.327 (< 2.22e-16)	-18.285 (< 2.22e-16)	-17.054 (< 2.22e-16)	-15.569 (3.3040e-13)	-18.327 (< 2.22e-16)	-17.907 (< 2.22e-16)	-16.776 (< 2.22e-16)	-15.826 (1.1724e-13	-18.285 (< 2.22e-16)	-18.050 (< 2.22e-16)	-17.411 (< 2.22e-16)	-15.953 (7.4607e-14)	-18.022 (< 2.22e-16)	-17.419 (< 2.22e-16)	-16.942 (< 2.22e-16)	-15.272 (4.4209e-13)
	OS	1000	0	1	1	2	8	8	7.5	7.5	8	7	4.75	1.5	9	9	8.25	9	7	7	8.5	6.5		-1.123 (1.0000)	-0.225 (1.0000)	-1.857 (0.9999)	18.061 (< 2.22e-16)	-11.288 (2.2706e-12	10.780 (2.8271e-11)	-8.027 (1.5116e-05)	18.490 (< 2.22e-16)	-17.683 (< 2.22e-16)	5.783 (0.0327)	-0.057 (1.0000)	-18.924 (< 2.22e-16)	-18.882 (< 2.22e-16)	-17.842 (< 2.22e-16)	-17.864 (< 2.22e-16)	-18.924 (< 2.22e-16)	-18.519 (< 2.22e-16)	-17.734 (< 2.22e-16)	17.864 (< 2.22e-16)	-18.882 (< 2.22e-16)	-18.653 (< 2.22e-16)	-18.154 (< 2.22e-16)	-17.928 (< 2.22e-16)	-18.618 (< 2.22e-16)	-18.074 (< 2.22e-16)	-17.864 (< 2.22e-16)	-17.864 (< 2.22e-16)
		100	0	1	1	2	8	8	7.5	7.5	8	7	4.75	1.5	9	9	8.25	9	7	7	8.5	6.5	0		-0.795 (1.0000)	-1.675 (1.0000)	17.694 (< 2.22e-16)	-8.695 (8.7473e-07)	10.544 (1.0099e-10	-7.912 (2.4108e-05)	18.097 (< 2.22e-16)	-16.975 (< 2.22e-16)	-4.772 (0.2993)	-0.080 (1.0000)	-18.504 (< 2.22e-16)	-18.465 (< 2.22e-16)	-17.489 (< 2.22e-16)	-17.510 (< 2.22e-16)	-18.504 (< 2.22e-16)	-18.125 (< 2.22e-16)	-17.387 (< 2.22e-16)	17.510 (< 2.22e-16)	-18.465 (< 2.22e-16)	-18.250 (< 2.22e-16)	-17.782 (< 2.22e-16)	-17.570 (< 2.22e-16)	-18.217 (< 2.22e-16)	-17.707 (< 2.22e-16)	17.510 (< 2.22e-16)	-17.510 (< 2.22e-16)
		10	0	1	1	2	8	8	7.5	7.5	8	7	4.75	1.5	9	9	8.25	9	7	7	8.5	6.5	0	0		-1.793 (1.0000)	14.627 (4.5086e-13	-5.631 (0.0485)	-8.162 (8.6396e-06)	-7.088 (0.0006)	16.746 (< 2.22e-16)	-12.648 (3.3551e-13)	-4.108 (0.6917)	-0.088 (1.0000)	-18.475 (< 2.22e-16)	-18.436 (< 2.22e-16)	-17.464 (< 2.22e-16)	-17.448 (< 2.22e-16)	-18.475 (< 2.22e-16)	-18.097 (< 2.22e-16)	-17.363 (< 2.22e-16)	-17.485 (< 2.22e-16)	-18.436 (< 2.22e-16)	-18.222 (< 2.22e-16)	-17.756 (< 2.22e-16)	-17.543 (< 2.22e-16)	-18.189 (< 2.22e-16)	-17.682 (< 2.22e-16)	-17.485 (< 2.22e-16)	-17.422 (< 2.22e-16)
		1	1	0	2	1	7	7	6.5	6.5	7	6	3.75	0.5	8	8	7.25	8	8	8	9.5	7.5	1	1	1		-6.253 (0.0086)	-0.662 (1.0000)	-6.148 (0.0118)	-7.101 (0.0005)	8.433 (2.7509e-06)	-4.986 (0.2041)	-0.709 (1.0000)	-1.591 (1.0000)	-18.473 (< 2.22e-16)	-18.434 (< 2.22e-16)	-17.463 (< 2.22e-16)	-17.109 (< 2.22e-16)	-18.473 (< 2.22e-16)	-18.096 (< 2.22e-16)	-17.361 (< 2.22e-16)	17.281 (< 2.22e-16)	-18.434 (< 2.22e-16)	-18.220 (< 2.22e-16)	-17.755 (< 2.22e-16)	-17.307 (< 2.22e-16)	-18.188 (< 2.22e-16)	-17.680 (< 2.22e-16)	-17.482 (< 2.22e-16)	-17.045 (< 2.22e-16)
	LE	1000	4	3	5	2	4	4	3.5	3.5	4	3	0.75	2.5	5	5	4.25	5	11	11	12.5	10.5	4	4	4	3		-16.626 (< 2.22e-16)	-16.270 (< 2.22e-16)	-11.141 (4.4377e-12	16.014 (< 2.22e-16)	-8.229 (6.5430e-06)	-8.415 (2.9622e-06)	-7.133 (0.0005)	-18.946 (< 2.22e-16)	-18.903 (< 2.22e-16)	-17.860 (< 2.22e-16)	-17.882 (< 2.22e-16)	-18.946 (< 2.22e-16)	-18.539 (< 2.22e-16)	17.752 (< 2.22e-16)	-17.882 (< 2.22e-16)	-18.903 (< 2.22e-16)	-18.673 (< 2.22e-16)	-18.172 (< 2.22e-16)	-17.946 (< 2.22e-16)	-18.638 (< 2.22e-16)	-18.093 (< 2.22e-16)	-17.882 (< 2.22e-16)	-17.882 (< 2.22e-16)
		100	1	0	2	1	7	7	6.5	6.5	7	6	3.75	0.5	8	8	7.25	8	8	8	9.5	7.5	1	1	1	0	3		-12.173 (4.3399e-13	-8.790 (5.7240e-07)	17.825 (< 2.22e-16)	-14.222 (5.4734e-13)	-1.097 (1.0000)	-1.670 (1.0000)	-18.503 (< 2.22e-16)	-18.464 (< 2.22e-16)	-17.488 (< 2.22e-16)	-17.509 (< 2.22e-16)	-18.503 (< 2.22e-16)	-18.124 (< 2.22e-16)	-17.386 (< 2.22e-16)	-17.509 (< 2.22e-16)	-18.464 (< 2.22e-16)	-18.249 (< 2.22e-16)	-17.781 (< 2.22e-16)	-17.569 (< 2.22e-16)	-18.217 (< 2.22e-16)	-17.706 (< 2.22e-16)	-17.509 (< 2.22e-16)	-17.509 (< 2.22e-16)
		10	4.5	5.5	3.5	6.5	12.5	12.5	12	12	12.5	11.5	9.25	6	13.5	13.5	12.75	13.5	2.5	2.5	4	2	4.5	4.5	4.5	5.5	8.5	5.5		-3.703 (0.8872)	17.206 (< 2.22e-16)	-15.263 (4.4742e-13)	-9.641 (1.0429e-08)	-3.609 (0.9176)	-18.472 (< 2.22e-16)	-18.433 (< 2.22e-16)	-17.462 (< 2.22e-16)	-17.191 (< 2.22e-16)	-18.472 (< 2.22e-16)	-18.095 (< 2.22e-16)	-17.360 (< 2.22e-16)	-17.442 (< 2.22e-16)	-18.433 (< 2.22e-16)	-18.219 (< 2.22e-16)	17.753 (< 2.22e-16)	-17.461 (< 2.22e-16)	-18.187 (< 2.22e-16)	17.679 (< 2.22e-16)	-17.482 (< 2.22e-16)	-17.173 (< 2.22e-16)
		1	9	10	8	11	17	17	16.5	16.5	17	16	13.75	10.5	18	18	17.25	18	2	2	0.5	2.5	9	9	9	10	13	10	4.5		-12.677 (3.2552e-13	-10.366 (2.6002e-10)	-8.223 (6.7148e-06)	-5.566 (0.0571)	-18.181 (< 2.22e-16)	-18.137 (< 2.22e-16)	-16.825 (< 2.22e-16)	-15.159 (4.9194e-13)	-18.181 (< 2.22e-16)	-17.744 (< 2.22e-16)	-16.508 (< 2.22e-16)	-15.379 (4.4342e-13	-18.137 (< 2.22e-16)	-17.891 (< 2.22e-16)	-17.220 (< 2.22e-16)	-15.499 (4.4764e-13)	-17.857 (< 2.22e-16)	-17.233 (< 2.22e-16)	-16.671 (< 2.22e-16)	-14.732 (5.0493e-13)
	OSLE	1000	5	4	6	3	3	3	2.5	2.5	3	2	0.25	3.5	4	4	3.25	4	12	12	13.5	11.5	5	5	5	4	1	4	9.5	14		-17.061 (< 2.22e-16)	-12.729 (3.1719e-13)	-9.473 (2.3677e-08)	-19.443 (< 2.22e-16)	-19.397 (< 2.22e-16)	-18.275 (< 2.22e-16)	-18.298 (< 2.22e-16)	-19.443 (< 2.22e-16)	-19.004 (< 2.22e-16)	-18.159 (< 2.22e-16)	-18.298 (< 2.22e-16)	-19.397 (< 2.22e-16)	-19.148 (< 2.22e-16)	-18.610 (< 2.22e-16)	-18.367 (< 2.22e-16)	19.111 (< 2.22e-16)	-18.524 (< 2.22e-16)	18.299 (< 2.22e-16=	-18.298 (< 2.22e-16)
		100	3.5	2.5	4.5	1.5	4.5	4.5	4	4	4.5	3.5	1.25	2	5.5	5.5	4.75	5.5	10.5	10.5	12	10	3.5	3.5	3.5	2.5	0.5	2.5	8	12.5	1.5		-6.026 (0.0168)	-5.559 (0.0580)	-18.566 (< 2.22e-16)	-18.526 (< 2.22e-16)	-17.541 (< 2.22e-16)	-17.562 (< 2.22e-16)	-18.566 (< 2.22e-16)	-18.183 (< 2.22e-16)	-17.438 (< 2.22e-16)	17.562 (< 2.22e-16)	-18.526 (< 2.22e-16)	-18.309 (< 2.22e-16)	17.837 (< 2.22e-16)	-17.622 (< 2.22e-16)	18.276 (< 2.22e-16)	-17.761 (< 2.22e-16)	-17.562 (< 2.22e-16)	-17.562 (< 2.22e-16)
		10	1.25	0.25	2.25	0.75	6.75	6.75	6.25	6.25	6.75	5.75	3.5	0.25	7.75	7.75	7	7.75	8.25	8.25	9.75	7.75	1.25	1.25	1.25	0.25	2.75	0.25	5.75	10.25	3.75	2.25		-2.199 (0.9999)	-18.475 (< 2.22e-16)	-18.435 (< 2.22e-16)	-17.464 (< 2.22e-16)	-17.434 (< 2.22e-16)	-18.475 (< 2.22e-16)	-18.097 (< 2.22e-16)	-17.362 (< 2.22e-16)	-17.483 (< 2.22e-16)	-18.435 (< 2.22e-16)	-18.222 (< 2.22e-16)	-17.756 (< 2.22e-16)	-17.537 (< 2.22e-16)	18.189 (< 2.22e-16)	-17.681 (< 2.22e-16)	-17.485 (< 2.22e-16)	-17.429 (< 2.22e-16)
		1	0	1	1	2	8	8	7.5	7.5	8	7	4.75	1.5	9	9	8.25	9	7	7	8.5	6.5	0	0	0	1	4	1	4.5	9	5	3.5	1.25		-18.472 (< 2.22e-16)	-18.433 (< 2.22e-16)	-17.462 (< 2.22e-16)	-16.892 (< 2.22e-16)	-18.472 (< 2.22e-16)	-18.095 (< 2.22e-16)	-17.360 (< 2.22e-16)	-0.505 (1.0000)	-18.433 (< 2.22e-16)	-18.219 (< 2.22e-16)	-17.754 (< 2.22e-16)	-17.144 (< 2.22e-16)	18.187 (< 2.22e-16)	-17.679 (< 2.22e-16)	-17.476 (< 2.22e-16)	-16.806 (< 2.22e-16)
POOR FORAGING CONDITIONS	US	1000	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105		-1.414 (1.0000)	-10.635 (6.2102e-11)	-10.340 (2.9841e-10)	-1.414 (1.0000)	-4.810 (0.2803)	-12.507 (3.5927e-13	10.340 (2.9847e-10	-1.414 (1.0000)	-3.799 (0.8503)	-7.518 (0.0001)	-9.591 (1.3321e-08)	-4.071 (0.7128)	-8.182 (7.9408e-06)	-10.340 (2.9832e-10	-10.340 (2.9835e-10)
		100	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0		-10.401 (2.1557e-10)	-10.111 (9.8229e-10)	-1.414 (1.0000)	-4.206 (0.6324)	-12.310 (3.9879e-13	10.113 (9.7050e-10	-0.010 (1.0000)	-3.074 (0.9934)	-7.158 (0.0004)	-9.338 (4.5285e-08)	-3.367 (0.9687)	-7.841 (3.2035e-05)	-10.101 (1.0314e-09	-10.111 (9.8211e-10)
		10	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0		-2.268 (0.9999)	-10.635 (6.2102e-11)	-8.003 (1.6631e-05)	-2.515 (0.9999)	-2.500 (0.9999)	-10.413 (2.0264e-10)	-8.950 (2.7647e-07)	-3.818 (0.8419)	-0.989 (1.0000)	-8.910 (3.3258e-07)	-4.240 (0.6114)	-0.481 (1.0000)	-2.457 (0.9999)
		1	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0		-10.340 (2.9841e-10)	-8.006 (1.6449e-05)	-0.273 (1.0000)	-0.040 (1.0000)	-10.113 (9.7036e-10)	-8.807 (5.2820e-07)	-5.148 (0.1479)	-1.027 (1.0000)	-8.650 (1.0672e-06)	-4.974 (0.2087)	-2.075 (0.9999)	-0.444 (1.0000)
	OS	1000	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0		-4.810 (0.2803)	12.507 (3.5927e-13	10.340 (2.9847e-10	-1.414 (1.0000)	-3.799 (0.8503)	-7.518 (0.0001)	-9.591 (1.3321e-08)	-4.071 (0.7128)	-8.182 (7.9408e-06)	-10.340 (2.9832e-10	-10.340 (2.9835e-10)
		100	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0		-10.238 (5.0717e-10	-8.070 (1.2651e-05)	-4.227 (0.6194)	-1.378 (1.0000)	-4.052 (0.7236)	-7.046 (0.0006)	-1.090 (1.0000)	-4.643 (0.3673)	-7.785 (3.9954e-05)	-8.030 (1.4891e-05)
		10	104	105	103	106	112	112	111.5	111.5	112	111	108.75	105.5	113	113	112.25	113	97	97	95.5	97.5	104	104	104	105	108	105	99.5	95	109	107.5	105.25	104	1	1	1	1	1	1		-0.512 (1.0000)	-12.329 (3.9413e-13)	-11.059 (6.2161e-12	-6.208 (0.0099)	-1.077 (1.0000)	-11.047 (6.6365e-12	-6.759 (0.0017)	-1.952 (0.9999)	-0.542 (1.0000)
		1	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1		-10.113 (9.7050e-10)	-8.842 (4.5306e-07)	-5.316 (0.1029)	-0.974 (1.0000)	-8.670 (9.7595e-07)	-5.129 (0.1538)	-2.280 (0.9999)	-0.505 (1.0000)
	LE	1000	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0		-3.084 (0.993)	-7.167 (0.0004)	-9.338 (4.5285e-08)	-3.396 (0.9644)	-7.858 (2.9962e-05)	-10.108 (9.9405e-10	-10.113 (9.7017e-10)
		100	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0		-5.187 (0.1363)	-7.912 (2.4078e-05)	-0.284 (1.0000)	-5.833 (0.0287)	-8.678 (9.4094e-07)	-8.812 (5.1745e-07)
		10	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0	0		-4.073 (0.7118)	-4.999 (0.1993)	-0.088 (1.0000)	-4.016 (0.7439)	-5.303 (0.1058)
		1	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0	0	0		-7.739 (4.7986e-05)	-3.788 (0.8548)	-0.926 (1.0000)	-1.313 (1.0000)
	OSLE	1000	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0	0	0	0		-5.735 (0.0371)	8.575 (1.4800e-06)	-8.652 (1.0565e-06)
		100	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0	0	0	0	0		-4.258 (0.6000)	-5.014 (0.1933)
		10	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0	0	0	0	0	0		-2.350 (0.9999)
		1	105	106	104	107	113	113	112.5	112.5	113	112	109.75	106.5	114	114	113.25	114	98	98	96.5	98.5	105	105	105	106	109	106	100.5	96	110	108.5	106.25	105	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	

Chapter 3

Appendix H – Model conceptualization: Parental provisioning dynamics of Cory’s shearwaters during chick rearing.

A) PURPOSE

The developed model intends to explore the parental provisioning dynamics of Cory’s shearwaters during the chick rearing period (from egg hatching to fledging of the young), considering physiologic and behaviour-based decisions of breeding parents upon contrasting environmental scenarios.

B) MODEL STRUCTURE AND FUNCTIONING

1. CHICK REARING SCHEDULE
2. FORAGING ALLOCATION DECISIONS
3. FORAGING TRIP DURATION
4. NEST ATTENDANCE DYNAMICS
5. ADULTS’ MASS GAINS AT SEA
6. ADULTS’ BODY CONDITION
7. MEAL SIZE
8. CHICK’ GROWTH
9. CHICK’ BODY CONDITION

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1. CHICK REARING SCHEDULE

The period of chick rearing, from egg hatching until the fledging of the young, in which the first days after hatching correspond to the guarding period and the last days before fledging correspond to the pre-fledging period. The time unit used in the model was the hour in order to capture short-term variations in the chick’ nutritional status, for a simulation extent of 2300 hours corresponding to the full period of chick rearing for the study species (i.e. 96 days) (Granadeiro 1991).

MODELLING ELEMENTS

- *Guarding period days* (Appendix I – “Constants”)
- *Pre-fledging period* (Appendix I – “Composed variables”)

Guarding period days

First 5 days after hatching, during which one of the parents remain with the chick until its thermoregulatory ability has developed (Granadeiro 1991).

Pre-fledging period

Last 15 days of chick rearing, during which breeding birds stimulate the emancipation of the offspring from the nest before fledging (Ramos et al. 2003).

2. FORAGING-ALLOCATION DECISIONS

The allocation of foraging effort by breeding Cory's shearwaters, in terms of typology of foraging trips, i.e. short foraging trips for provisioning (‘*provisioning’*; Appendix I – “Constants”) *versus* long foraging trips for self-feeding (‘*self-feeding’*; Appendix I– “Constants”). The model was prepared to simulate four hypotheses regarding potential mechanisms driving Cory's shearwaters foraging allocation-decisions (FADs).

MODELLING ELEMENTS

- *FAD1* (Figure 1, Appendix I – “Switcher”)
- *FAD2* (Figure 1, Appendix I – “Switcher”)
- *FAD3* (Figure 1, Appendix I – “Switcher”)
- *FAD4* (Figure 1, Appendix I – “Switcher”)

FAD 1

Provisioning is determined by the adult' body mass threshold for reproduction.

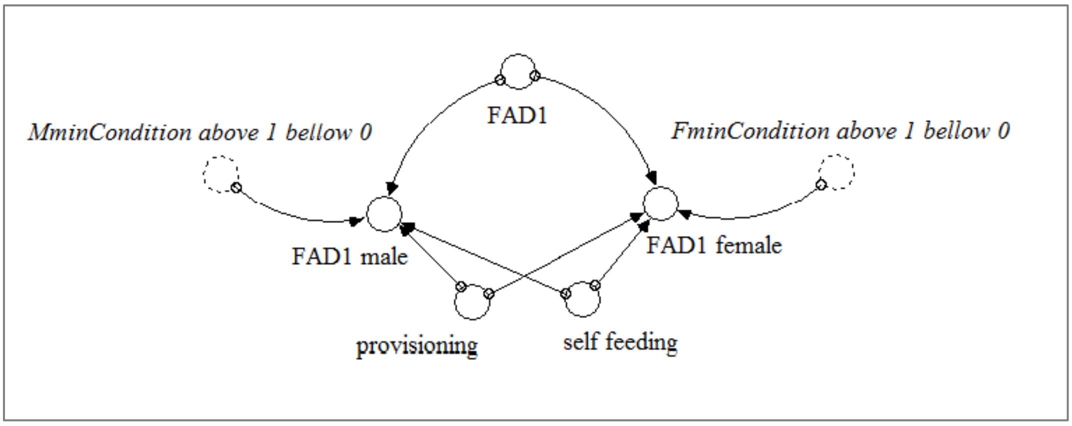


Figure 1. Conceptual diagram of the sub-model of ‘Foraging-allocation decisions’. External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables' equations are expressed in Appendix I.

MODELLING ELEMENTS

- *FAD1 male* (Figure 1, Appendix I – “Composed variables”)
- *FAD1 female* (Figure 1, Appendix I – “Composed variables”)
- *MminCondition above 1 bellow 0* (Figure 1, Appendix I – “Composed variables”)
- *FminCondition above 1 bellow 0* (Figure 1, Appendix I – “Composed variables”)
- *Provisioning* (Figure 1, Appendix I – “Constants”)
- *self feeding* (Figure 1, Appendix I – “Constants”)

FAD1 male / FAD1 female

If the adult' body mass threshold for reproduction has not been reached (see ‘*MminCondition above 1 bellow 0’* / *‘FminCondition above 1 bellow 0’* in section ‘6. Adults' body condition’), breeding birds prioritize provisioning, otherwise self-feeding is assured.

FAD 2

Provisioning is determined by short-term variations in chick's nutritional status.

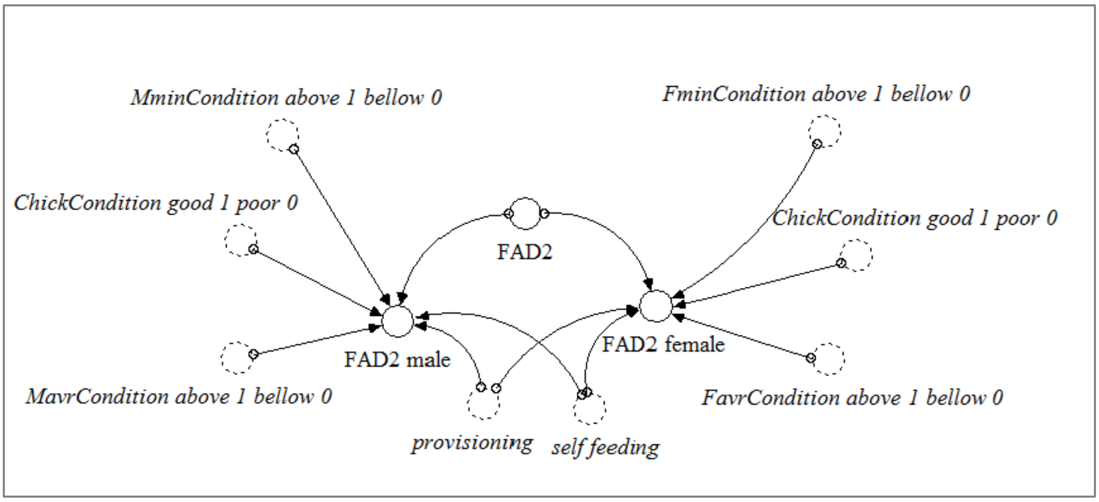


Figure 2. Conceptual diagram of the sub-model of 'Foraging-allocation decisions'. External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables' equations are expressed in Appendix I.

MODELLING ELEMENTS

- *FAD2 male* (Figure 2, Appendix I – "Composed variables")
- *FAD2 female* (Figure 2, Appendix I – "Composed variables")
- *MminCondition above 1 bellow 0* (Figure 2, Appendix I – "Composed variables")
- *FminCondition above 1 bellow 0* (Figure 2, Appendix I – "Composed variables")
- *ChickCondition good 1 poor 0* (Figure 2, Appendix I – "Composed variables")
- *MavrCondition above 1 bellow 0* (Figure 2, Appendix I – "Composed variables")
- *FavrCondition above 1 bellow 0* (Figure 2, Appendix I – "Composed variables")
- *Provisioning* (Figure 2, Appendix I – "Constants")
- *self feeding* (Figure 2, Appendix I – "Constants")

FAD2 male / FAD2 female

Based on FAD1, if the adult' body mass threshold for reproduction has not been reached, birds evaluate the nutritional status of their chick (see '*ChickCondition good 1 poor 0'* in section 8. 'Chick body condition'). Parents of chicks in poor nutritional conditions increase foraging effort by prioritizing provisioning. Whenever the chick is in good nutritional condition, if the adult is in poor body condition self-feeding is assured (see '*MavrCondition above 1 bellow 0' / 'FavrCondition above 1 bellow 0'* in section 6. 'Adults' body condition'). Otherwise, provisioning is prioritized.

FAD 3

Provisioning is determined in response to the partner' allocation decision.

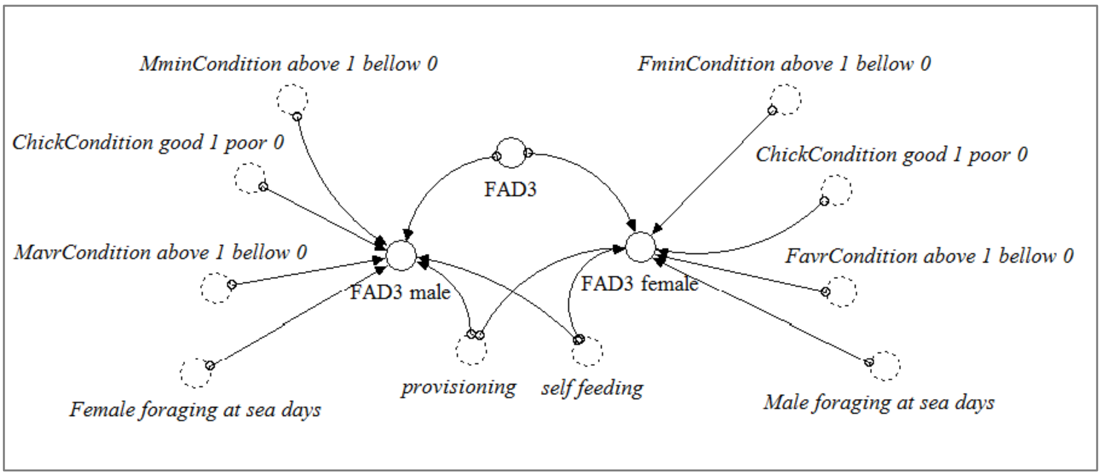


Figure 3. Conceptual diagram of the sub-model of 'Foraging-allocation decisions'. External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables' equations are expressed in Appendix I.

MODELLING ELEMENTS

- *FAD3 male* (Figure 3, Appendix I – "Composed variables")
- *FAD3 female* (Figure 3, Appendix I – "Composed variables")
- *MminCondition above 1 bellow 0* (Figure 3, Appendix I – "Composed variables")
- *FminCondition above 1 bellow 0* (Figure 3, Appendix I – "Composed variables")
- *ChickCondition good 1 poor 0* (Figure 3, Appendix I – "Composed variables")
- *MavrCondition above 1 bellow 0* (Figure 3, Appendix I – "Composed variables")
- *FavrCondition above 1 bellow 0* (Figure 3, Appendix I – "Composed variables")
- *Male foraging at sea days* (Figure 3, Appendix I – "Composed variables")
- *Female foraging at sea days* (Figure 3, Appendix I – "Composed variables")
- *provisioning* (Figure 3, Appendix I – "Constants")
- *self feeding* (Figure 3, Appendix I – "Constants")

FAD3 male / FAD3 female

Based on FAD2, parents of chicks in poor nutritional conditions evaluate the partners' allocation decision (see '*Male foraging at sea days' / 'Female foraging at sea days'* in section 6 'Nest attendance dynamics'). If the partner is engaged in a long trip, provisioning is ensured; otherwise, if the partner is engaged in provisioning, birds evaluate their own body condition (see '*MavrCondition above 1 bellow 0' / 'FavrCondition above 1 bellow 0'* in section 6. 'Adults' body condition'). If the adult is in a poor body condition self-feeding is prioritized, otherwise provisioning is ensured.

FAD 4

Provisioning is determined in response to both the partner' allocation decision and body condition.

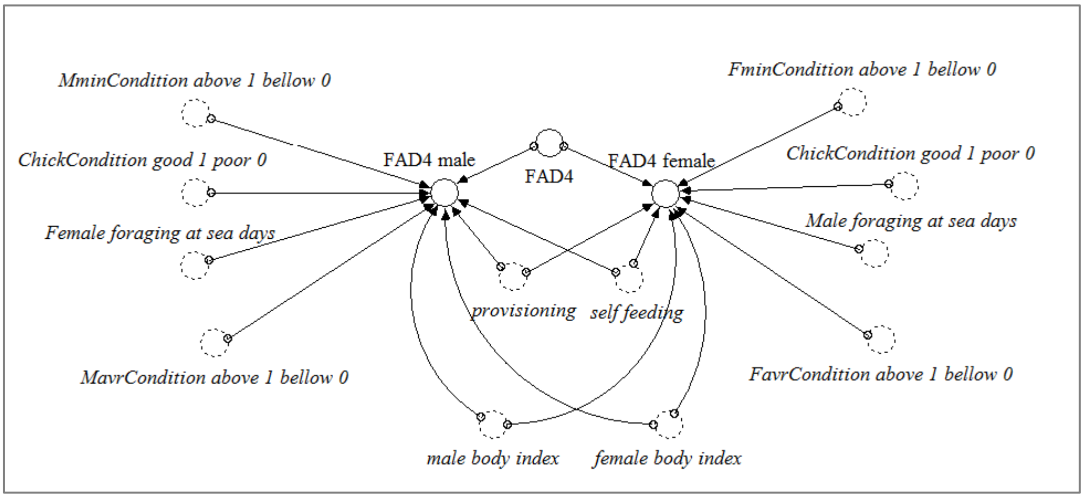


Figure 4. Conceptual diagram of the sub-model of 'Foraging-allocation decisions'. External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables' equations are expressed in Appendix I.

MODELLING ELEMENTS

- *FAD4 male* (Figure 4, Appendix I – "Composed variables")
- *FAD4 female* (Figure 4, Appendix I – "Composed variables")
- *MminCondition above 1 bellow 0* (Figure 4, Appendix I – "Composed variables")
- *FminCondition above 1 bellow 0* (Figure 4, Appendix I – "Composed variables")
- *ChickCondition good 1 poor 0* (Figure 4, Appendix I – "Composed variables")
- *MavrCondition above 1 bellow 0* (Figure 4, Appendix I – "Composed variables")
- *FavrCondition above 1 bellow 0* (Figure 4, Appendix I – "Composed variables")
- *Male foraging at sea days* (Figure 4, Appendix I – "Composed variables")
- *Female foraging at sea days* (Figure 4, Appendix I – "Composed variables")
- *male body index* (Figure 4, Appendix I – "Composed variables")
- *female body index* (Figure 4, Appendix I – "Composed variables")
- *provisioning* (Figure 4, Appendix I – "Constants")
- *self feeding* (Figure 4, Appendix I – "Constants")

FAD4 male / FAD4 female

Based on FAD 3, parents of chicks in poor nutritional conditions whose partner is engaged in provisioning evaluate each other condition. If the adult presents a good body condition provisioning is ensured (see '*MavrCondition above 1 bellow 0' / 'FavrCondition above 1 bellow 0'* in section 6. 'Adults' body condition'. However, if the adult is in a poor condition, self-maintenance is prioritized only if its own body condition is poorer than the partner's (see '*male body index' / 'female body index'* in section 6. 'Adults' body condition'). Otherwise, provisioning is assured.

3. FORAGING TRIP DURATION

The duration of foraging trips by males and females. After the selection of a given typology of foraging trip (i.e. provisioning or self-feeding), the model randomly generates the respective foraging trip duration, in days, according to probabilistic curves of real data for short and long foraging trips. The probabilistic curves of short (≤ 3 days) and long foraging trips (> 3 days) were calibrated taking into account the frequency distribution of foraging trip duration at Selvagem Grande, assuming 5 days as the average duration of long foraging trips (Granadeiro et al., 1998a).

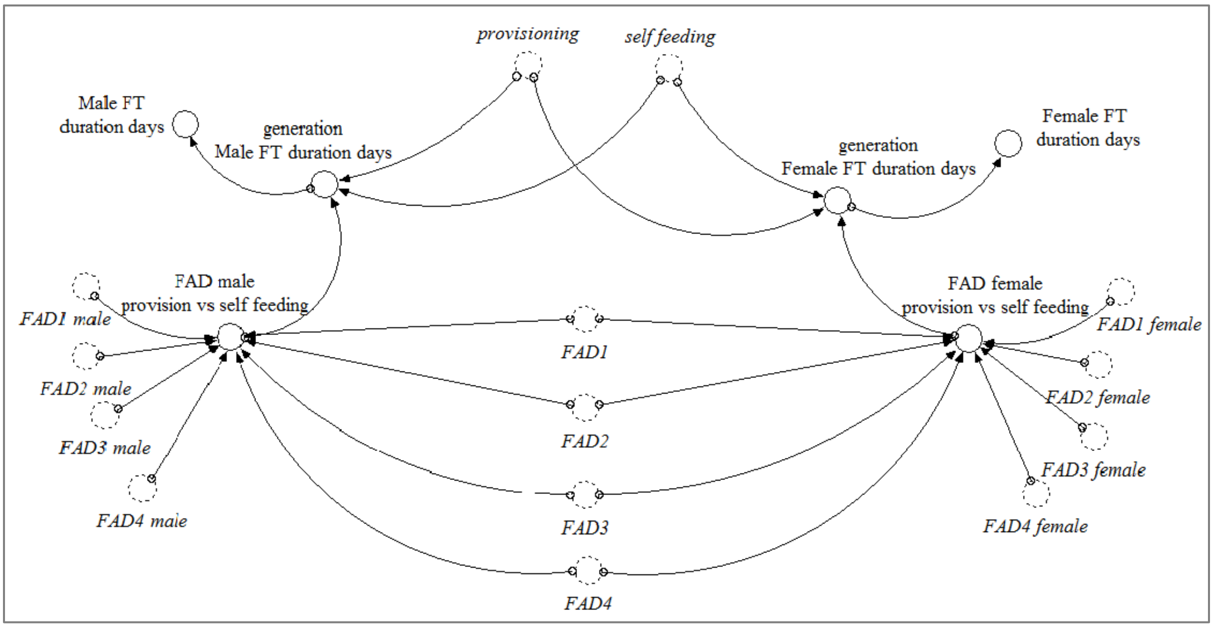


Figure 5. Conceptual diagram of the sub-model of ‘Foraging trip duration’. External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables’ equations are expressed in Appendix I.

MODELLING ELEMENTS

- *FAD male provision vs self feeding* (Figure 5, Appendix I – “Composed variables”)
- *FAD female provision vs self feeding* (Figure 5, Appendix I – “Composed variables”)
- *generation Male FT duration days* (Figure 5, Appendix I – “Composed variables”)
- *generation Female FT duration days* (Figure 5, Appendix I – “Composed variables”)
- *Male FT duration days* (Figure 5, Appendix I – “Composed variables”)
- *Female FT duration days* (Figure 5, Appendix I – “Composed variables”)

FAD male provision vs self feeding / FAD female provision vs self feeding

The decision of males and females in terms of typology of foraging trips, i.e. short foraging trips for provisioning *versus* long foraging trips for self-feeding, according to the allocation decision considered.

generation Male FT duration days / generation Female FT duration days

The probabilistic curves of short (≤ 3 days) and long foraging trips (> 3 days), taking into account the frequency distribution of foraging trips duration at Selvagem Grande (Granadeiro et al. 1998).

Male FT duration days / Female FT duration days

The duration of foraging trips, in days, by males and females.

4. NEST ATTENDANCE DYNAMICS

Dynamics of nest attendance by males and females considering the time, in hours, that each parent remain foraging at sea.

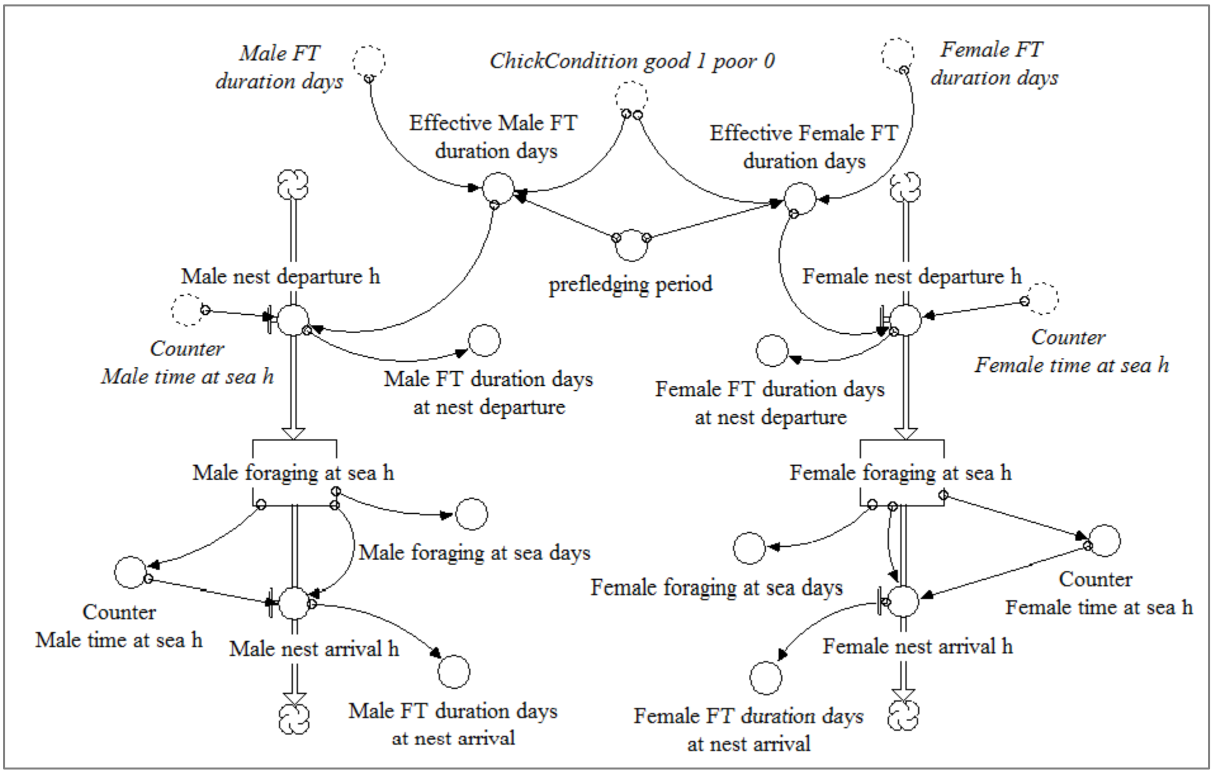


Figure 6. Conceptual diagram of the sub-model of ‘Nest attendance Dynamics’. Rectangles represent the state variables; External variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between variables are fine arrows. The specification of all variables’ equations are expressed in Appendix I.

STATE VARIABLES

4.1. MALE FORAGING AT SEA H / FEMALE FORAGING AT SEA H (Figure 6, Appendix I – “Difference Equations”**)**

PROCESSES

4.1.1. MALE NEST DEPARTURE H / FEMALE NEST DEPARTURE H (Figure 6, Appendix I – “Process Equations”**)**

4.1.2. MALE NEST ARRIVAL H / FEMALE NEST ARRIVAL H (Figure 6, Appendix I – “Process Equations”**)**

4.1.1. MALE NEST DEPARTURE H / FEMALE NEST DEPARTURE H

Nest departure of males and females for a new foraging trip, considering the time, in hours, that each parent will remain foraging at sea. These variables are updated, in days, through the variables ‘*Male FT duration days at nest departure*’ and *‘Female FT duration days at nest departure’* (Figure 6, Appendix I – “Composed variables”).

MODELLING ELEMENTS

- *Effective Male FT duration days* (Figure 6, Appendix I – “Composed variables”)
- *Effective Female FT duration days* (Figure 6, Appendix I – “Composed variables”)
- *Counter Male time at sea h* (Figure 6, Appendix I – “Other Variables”)
- *Counter Female time at sea h* (Figure 6, Appendix I – “Other Variables”)

Effective Male FT duration days / Effective Female FT duration days

This variable adjusts the duration of foraging trips by males and females, taking into account the chick body condition (see ‘*ChickCondition good 1 poor 0’* in section 8. ‘Chick body condition’) at emancipation from the nest before fledging (see ‘*prefledging period’* in section 1. ‘Breeding schedule’). In the last 15 days of chick rearing, parents of chicks in good nutritional condition prioritize longer journeys in order to replenish self-reserves for migration and trigger the necessary stimulus for young birds to leave the nest (Ramos et al. 2003).

Counter Male time at sea h / Counter Female time at sea h

The time of the simulation that elapses between the moment of departure until the arrival at the nest.

4.1.2. MALE NEST ARRIVAL / FEMALE NEST ARRIVAL

Nest arrival of males and females after a foraging trip, considering the time, in hours, that each parent remained foraging at sea. These variables are updated in days through the variables ‘*Male FT duration days at nest arrival’* and *‘Female FT duration days at nest arrival’* (Figure 6, Appendix I – “Composed variables”).

MODELLING ELEMENTS

- *Male foraging at sea h* (Figure 6, Appendix I – “Difference equations”)
- *Female foraging at sea h* (Figure 6, Appendix I – “Difference equations”)
- *Counter Male time at sea h* (Figure 6, Appendix I – “Other Variables”)
- *Counter Female time at sea h* (Figure 6, Appendix I – “Other Variables”)

Male foraging at sea h / Female foraging at sea h

The time, in hours, that each parent remains foraging at sea. These variables are updated, in days, through the variables ‘*Male foraging at sea days’* and *‘Female foraging at sea days’* (Figure 6, Appendix I – “Composed variables”).

Counter Male time at sea h / Counter Female time at sea h

The time of the simulation that elapses between the moment of departure until the arrival at the nest.

5. ADULTS' MASS GAINS AT SEA

Variations in the body weight of adult birds throughout chick rearing. As initial simulations settings, males were assumed to weight 946.8 grams and females 836.1 grams, considering the average weight of males and females breeding at Selvagem Grande (Granadeiro 1993).

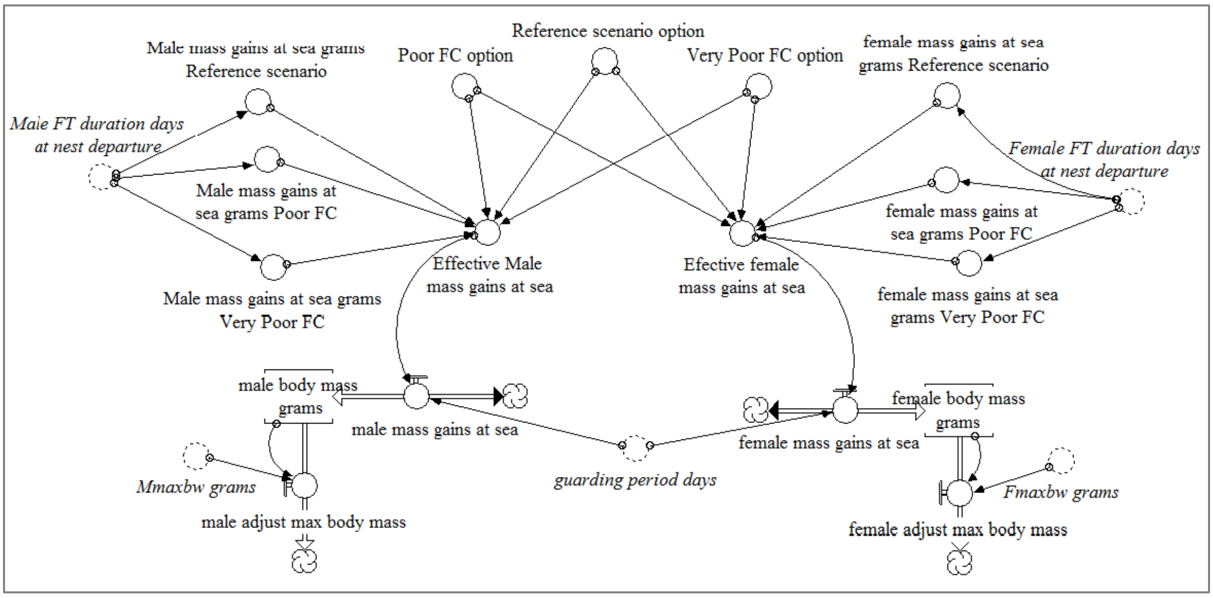


Figure 7. Conceptual diagram of the sub-model of 'Adults' mass gains at sea'. Rectangles represent the state variables; External variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between variables are fine arrows. The specification of all variables' equations are expressed in Appendix I.

STATE VARIABLES

5.1. MALE BODY MASS GRAMS / FEMALE BODY MASS GRAMS (Figure 7, Appendix I – "Difference Equations"**)**

PROCESSES

5.1.1. MALE MASS GAINS AT SEA / FEMALE MASS GAINS AT SEA (Figure 6, Appendix I – "Process Equations"**)**

5.1.2. MALE ADJUST MAX BODY MASS / FEMALE ADJUST MAX BODY MASS (Figure 6, Appendix I – "Process Equations"**)**

5.1.1. MALE MASS GAINS AT SEA / FEMALE MASS GAINS AT SEA

Mass gains at sea by male and female birds in relation to the duration of foraging trips. Each parent was assumed to remain in the nest half of the guarding period (see '*guarding period days'* in section 1. 'Breeding schedule'), by indirectly considering a decrease of 50% in the energetic costs of foraging trips during this period (i.e. breeding birds loose half of the expected weight in foraging trips performed during the guarding stage).

MODELLING ELEMENTS

- *Effective Male mass gains at sea* (Figure 7, Appendix I – "Composed variables")

- *Effective Female mass gains at sea* (Figure 7, Appendix I – “Composed variables”)
- *guarding period days* (Figure 7, Appendix I – “Constants”)

Effective Male mass gains at sea / Effective Female mass gains at sea
Mass gains at sea by males and females in relation to the duration of foraging trips, according to the environmental scenario considered.

MODELLING ELEMENTS

- *Reference scenario option* (Figure 7, Appendix I – “Switcher”)
- *Poor FC option* (Figure 7, Appendix I – “Switcher”)
- *Very Poor FC option* (Figure 7, Appendix I – “Switcher”)
- *Male mass gains at sea grams Reference scenario* (Figure 7, Appendix I – “Composed variables”)
- *Male mass gains at sea grams Poor FC* (Figure 7, Appendix I – “Composed variables”)
- *Male mass gains at sea grams Very Poor FC* (Figure 7, Appendix I – “Composed variables”)
- *Female mass gains at sea grams Reference scenario* (Figure 7, Appendix I – “Composed variables”)
- *Female mass gains at sea grams Poor FC* (Figure 7, Appendix I – “Composed variables”)
- *Female mass gains at sea grams Very Poor FC* (Figure 7, Appendix I – “Composed variables”)

Male mass gains at sea grams Reference scenario/ Female mass gains at sea grams Reference scenario
Changes in the body mass of males and females, given the mass gains at sea in relation to the duration of incubation shifts, obtained from birds breeding at Selvagem Grande (Ramos et al. 2009).

Male mass gains at sea grams Poor FC/ Female mass gains at sea grams Poor FC
Changes in the body mass of males and females, given the central value between the lower limit and the average mass gains in relation to the duration of incubation shifts, obtained from birds breeding at Selvagem Grande (Ramos et al. 2009).

Male mass gains at sea grams Very Poor FC/ Female mass gains at sea grams Very Poor FC
Changes in the body mass of males and females, given the lower limit of mass gains in relation to the duration of incubation shifts, obtained from birds breeding at Selvagem Grande (Ramos et al. 2009).

5.1.2. MALE ADJUST MAX BODY MASS / FEMALE ADJUST MAX BODY MASS

This process adjust the weight of adult birds taking into account the maximum possible weight of an individual bird (see ‘*Mmaxbw grams’ / ’Fmaxbw grams’* in section 6. ‘Adults’ body condition’).

MODELLING ELEMENTS

- *male body mass grams* (Figure 7, Appendix I – “Difference Equations”)
- *female body mass grams* (Figure 7, Appendix I – “Difference Equations”)
- *Mmaxbw grams* (Figure 7, Appendix I – “Constants”)
- *Fmaxbw grams* (Figure 7, Appendix I – “Constants”)

male body mass grams / female body mass grams

The body weight of adult birds., in grams, throughout chick rearing.

6. ADULTS’ BODY CONDITION

The body condition of adult birds, taking into account the availability of fat reserves to reproduction (qualitative assessment), and the amount of stored body reserves (quantitative assessment). In particular, adult birds admit lowering their body condition up to 12% of their average weight (hereinafter, adults’ body mass threshold for reproduction), considering the safety margin of fat reserves retained by Sooty shearwaters throughout chick rearing (Weimerskirch 1998). The initial weight of adult birds was assumed to represent the body mass that individuals intend to maintain, on average, throughout the chick rearing period. Therefore, an adult bird was considered in a good body condition whenever its body mass was greater than its initial weight and, in contrast, in a poor condition when its body mass was bellow that reference value. Furthermore, so that birds can compare body condition with that of their partner in FAD 4, an index that is continuously updated throughout chick rearing measures the proportion of variation in each parent’ body mass in relation to their initial weight.

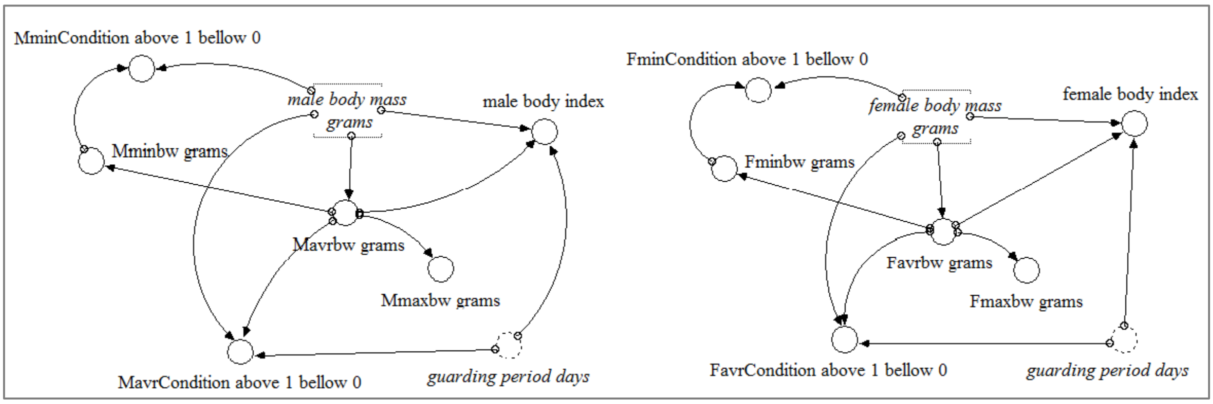


Figure 8. Conceptual diagram of the sub-model of ‘Adults’ body condition’. Rectangles represent the state variables; External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables’ equations are expressed in Appendix I.

MODELLING ELEMENTS

- *Mminbw grams* (Figure 8, Appendix I – “Constants”)
- *Mavrbw grams* (Figure 8, Appendix I – “Constants”)
- *Mmaxbw grams* (Figure 8, Appendix I – “Constants”)
- *MminCondition above 1 bellow 0* (Figure 8, Appendix I – “Composed Variables”)
- *MavrCondition above 1 bellow 0* (Figure 8, Appendix I – “Composed Variables”)
- *male body index* (Figure 8, Appendix I – “Composed Variables”)
- *Fminbw grams* (Figure 8, Appendix I – “Constants”)
- *Favrbw grams* (Figure 8, Appendix I – “Constants”)
- *Fmaxbw grams* (Figure 8, Appendix I – “Constants”)
- *FminCondition above 1 bellow 0* (Figure 8, Appendix I – “Composed Variables”)
- *FavrCondition above 1 bellow 0* (Figure 8, Appendix I – “Composed Variables”)
- *female body index* (Figure 8, Appendix I – “Composed Variables”)
- *guarding period days* (Figure 8, Appendix I – “Constants”)

Mminbw grams / Fminbw grams
The minimum possible weight of adult birds (i.e. adult' body mass threshold for reproduction), considering the proportion of body mass reserves that birds admit to spend in reproduction (i.e. 12% below their initial weight) (Weimerskirch 1998).

Mavrbw grams / Favrnbw grams
The initial weight of adult birds.

Mmaxbw grams / Fmaxbw grams
The maximum possible weight of adult birds, considering the proportion of body mass reserves that birds can store during reproduction (i.e. 12% above their initial weight) (Weimerskirch 1998).

MminCondition above 1 bellow 0 / FminCondition above 1 bellow 0
The body condition of adult birds, in terms of availability of fat reserves to reproduction, given the adult' body mass threshold for reproduction.

MavrCondition above 1 bellow 0 / FavrCondition above 1 bellow 0
The body condition of adult birds, in terms of the amount of fat reserves, given the initial adult' body mass (i.e. in the beginning of chick rearing).

male body index / female body index
The body condition of adult birds, given the proportion of variation in body mass in relation to initial weight (i.e. in the beginning of chick rearing). During the guarding period, parents favoured provisioning (short trips) independently of the foraging allocation decision considered.

7. MEAL SIZE

The amount of food delivered by each parent to the chick. Meal sizes were attributable to the duration of foraging trips, based on data from Cory's shearwaters breeding at Selvagem Grande (Granadeiro et al. 1998). The delivery of meals to the chicks was restricted to a single parent during the guarding period (see '*guarding period days'* in section 1. 'Breeding schedule).

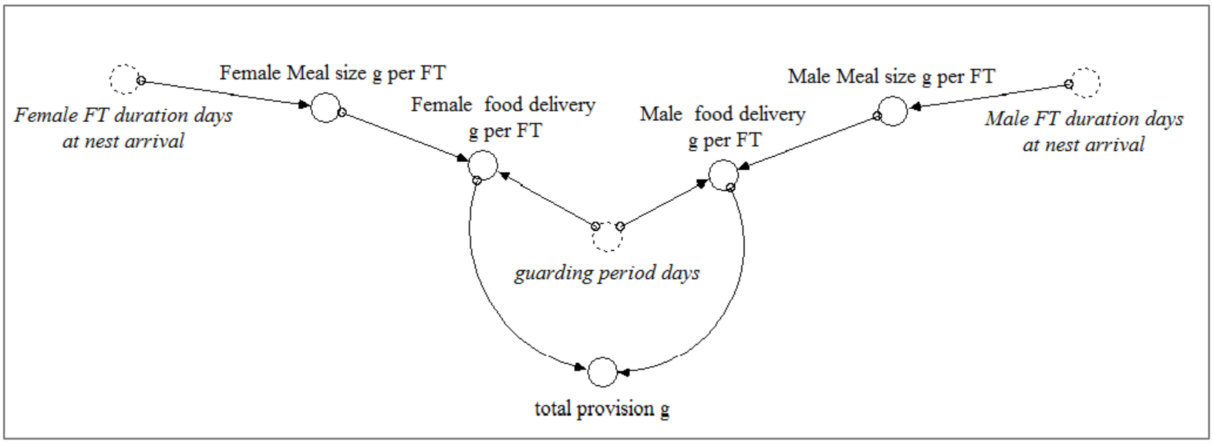


Figure 9. Conceptual diagram of the sub-model of ‘Meal size’. External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables’ equations are expressed in Appendix I.

MODELLING ELEMENTS

- *Male Meal size g per FT* (Figure 9, Appendix I – “Composed Variables”)
- *Male food delivery g per FT* (Figure 9, Appendix I – “Composed Variables”)
- *Female Meal size g per FT* (Figure 9, Appendix I – “Composed Variables”)
- *Female food delivery g per FT* (Figure 9, Appendix I – “Composed Variables”)
- *total provision g* (Figure 9, Appendix I – “Composed Variables”)
- *guarding period days* (Figure 9, Appendix I – “Constants”)

Male Meal size g per FT / Female Meal size g per FT

Meal sizes attributable to the duration of foraging trips, based on data from Cory’s shearwaters breeding at Selvagem Grande (Granadeiro et al. 1998).

Male food delivery g per FT / Female food delivery g per FT

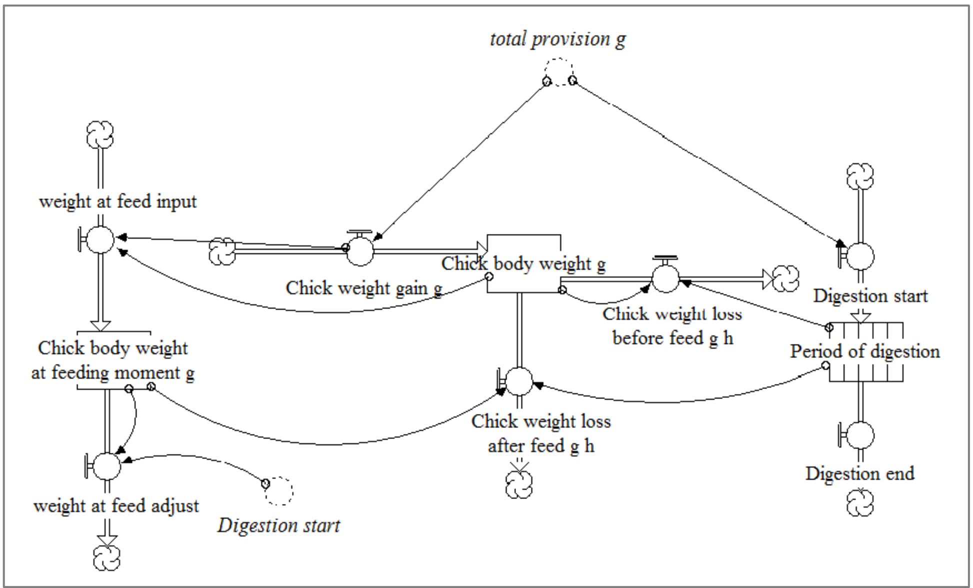
Delivery of meals to the chicks restricted to a single parent during the guarding period.

total provision g

Total amount of food delivered by both parents.

8. CHICK GROWTH

Offspring growth given the balance between gains from provisioning and physiologic/metabolic losses. The chick’ body weight (in grams) was calculated throughout chick rearing considering the



balance between gains from provisioning, given by the total amount of food delivered by both parents, and physiological and metabolic losses (in terms of mass) due to defecation, respiration and digestion (Walsberg and Carey 2006). Since the chick spend more energy in digestion and excretion in the first hours after receiving a meal, we account for time-dependent variations in food assimilation efficiency, i.e. the rate of weight loss was greater within the 4h after being feed, decreasing afterwards (Hamer et al. 1999).

Figure 10. Conceptual diagram of the sub-model of ‘Chick growth’. Rectangles represent the state variables; External variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between variables are fine arrows. The specification of all variables’ equations are expressed in Appendix I.

STATE VARIABLES

8.1. PERIOD OF DIGESTION (Figure 10, Appendix I – “Difference Equations”)
8.2. CHICK BODY WEIGHT AT FEEDING MOMENT G (Figure 10, Appendix I – “Difference Equations”)
8.3. CHICK BODY WEIGHT G (Figure 10, Appendix I – “Difference Equations”)

8.1. PERIOD OF DIGESTION

The period of 4 hours after feeding.

PROCESSES

8.1.1. DIGESTION START (Figure 10, Appendix I – “Process Equations”)
8.1.2. DIGESTION END (Figure 10, Appendix I – “Process Equations”)

8.1.1./.2. DIGESTION START / DIGESTION END

Digestion starts at provisioning and lasts 4 hours.

8.2. CHICK BODY WEIGHT AT FEEDING MOMENT G

The body weight of chick at feeding moment.

PROCESSES

8.2.1. WEIGHT AT FEED INPUT (Figure 10, Appendix I – “Process Equations”)
8.2.2. WEIGHT AT FEED ADJUST (Figure 10, Appendix I – “Process Equations”)

8.2.1. WEIGHT AT FEED INPUT

The chick body mass at provisioning.

8.2.2. WEIGHT AT FEED ADJUST

This variable update the chick body mass between feeding events.

8.3. CHICK BODY WEIGHT G

The chick body weight, in grams, throughout chick rearing.

PROCESSES

8.3.1. CHICK WEIGHT GAIN G (Figure 10, Appendix I – “Process Equations”)
8.3.2. CHICK WEIGHT LOSS AFTER FEED G H (Figure 10, Appendix I – “Process Equations”)
8.3.3. CHICK WEIGHT LOSS BEFORE FEED G H (Figure 10, Appendix I – “Process Equations”)

8.3.1. CHICK WEIGHT GAIN G

Gains, in mass, from provisioning (see '*total provision g'* in section 7. 'Meal size').

8.3.2. CHICK WEIGHT LOSS AFTER FEED G H

Food assimilation efficiency during digestion (4 hours after feeding).

8.3.3. CHICK WEIGHT LOSS BEFORE FEED G H

Food assimilation efficiency after digestion (after 4 hours from feeding).

9. CHICK BODY CONDITION

The chick body condition, taking into account the optimal growth rate of nestlings. An empirical growth curve of real chicks under optimal conditions (Quillfeldt et al. 2007) was used to evaluate the body condition of nestlings throughout chick rearing. The chick was considered in a good nutritional condition whenever its weight was greater than the optimal weight, and in a poor condition whenever lower than the optimal weight.

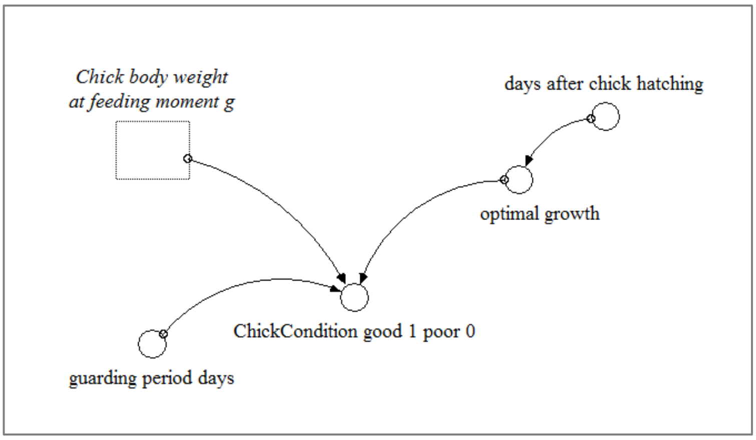


Figure 11. Conceptual diagram of the sub-model of 'Chick body condition. Rectangles represent the state variables; External variables, parameters or constants are small circles; all the relations between variables are fine arrows. The specification of all variables' equations are expressed in Appendix I.

MODELING ELEMENTS

- *Chick Condition good 1 poor 0* (Figure 11, Appendix I – "Composed Variables")
- *guarding period days* (Figure 11, Appendix I – "Constants")
- *chick body weight at feeding moment g* (Figure 10, Appendix I – "Difference Equations")
- *optimal growth* (Figure 11, Appendix I – "Composed Variables")

Chick Condition good 1 poor 0

The chick body condition at provisioning (i.e. chick body mass perceived by either parent at the moment of a feed), using as reference the chick daily food requirements for optimal growth. During the guarding period (see '*guarding period days'* in section 1. 'Breeding schedule') chicks were assumed to present poor body condition.

optimal growth

Optimal chick growth according to age (‘*days after chick hatching’*, Figure 11, Appendix I – “Other variables”), using the empirical growth curve of real chicks under optimal conditions (Quillfeldt et al. 2007).

optimal growth = (26.31 + 33.36 * ‘*days after chick hatching’* - 0.26 * (‘*days after chick hatching’* ^2))

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Appendix I - Specification of all mathematic equations included in the model.

DIFFERENCE EQUATIONS

Nest attendance dynamics

Male_foraging_at_sea_h(t) = Male_foraging_at_sea_h(t - dt) + (Male_nest_departure_h - Male_nest_arrival_h) * dt

Female_foraging_at_sea_h(t) = Female_foraging_at_sea_h(t - dt) + (Female_nest_departure_h - Female_nest_arrival_h) * dt

Adults' mass gains at sea

male_body_mass_grams(t) = male_body_mass_grams(t - dt) + (male_mass_gains_at_sea - male_adjust_max_body_mass) * dt

female_body_mass_grams(t) = female_body_mass_grams(t - dt) + (female_mass_gains_at_sea - female_adjust_max_body_mass) * dt

Chick growth

Period_of_digestion(t) = Period_of_digestion(t - dt) + (Digestion_start - Digestion_end) * dt

Chick_body_weight_at_feeding_moment_g(t) = Chick_body_weight_at_feeding_moment_g(t - dt) + (weight_at_feed_input - weight_at_feed_adjust) * dt

Chick_body_weight_g(t) = Chick_body_weight_g(t - dt) + (Chick_weight_gain_g - Chick_weight_loss_before_feed_g_h - Chick_weight_loss_after_feed_g_h) * dt

PROCESS EQUATIONS

Nest attendance dynamics

```
INIT Male_foraging_at_sea_h = 0
INFLOWS:
Male_nest_departure_h = IF (Counter_Male_time_at_sea_h = 0 )
  THEN Effective_Male_FT_duration_days*24
  ELSE 0
OUTFLOWS:
Male_nest_arrival_h =
IF Counter_Male_time_at_sea_h = 0
THEN Male_foraging_at_sea_h
ELSE 0
```

```
INIT Female_foraging_at_sea_h = 0
INFLOWS:
Female_nest_departure_h = IF (Counter_Female_time_at_sea_h = 0 )
  THEN Effective_Female_FT_duration_days*24
  ELSE 0
OUTFLOWS:
Female_nest_arrival_h =
IF Counter_Female_time_at_sea_h = 0
THEN Female_foraging_at_sea_h
ELSE 0
```

Adults' mass gains at sea

```
INIT male_body_mass_grams = 946.8
INFLOWS:
male_mass_gains_at_sea = IF TIME<guarding_period_days*24 THEN
Effective_Male_mass_gains_at_sea/2 ELSE Effective_Male_mass_gains_at_sea
OUTFLOWS:
male_adjust_max_body_mass = IF male_body_mass_grams>Mmaxbw_grams THEN
(male_body_mass_grams-Mmaxbw_grams) ELSE 0
```

```
INIT female_body_mass_grams = 836.1
INFLOWS:
female_mass_gains_at_sea = IF TIME<guarding_period_days*24 THEN
Efective_female_mass_gains_at_sea/2 ELSE Efective_female_mass_gains_at_sea
```

```
OUTFLOWS:
female_adjust_max_body_mass = IF female_body_mass_grams>Fmaxbw_grams THEN
(female_body_mass_grams-Fmaxbw_grams) ELSE 0
```

Chick growth

```
INIT Period_of_digestion = 0
            TRANSIT TIME = 4
            CAPACITY = INF
            INFLOW LIMIT = INF
INFLOWS:
Digestion_start = IF total_provision_g=0 THEN 0 ELSE 1
OUTFLOWS:
Digestion_end = CONVEYOR OUTFLOW
```

```
INIT Chick_body_weight_at_feeding_moment_g = 0
INFLOWS:
weight_at_feed_input = IF Chick_weight_gain_g >0
THEN Chick_body_weight_g
ELSE 0
OUTFLOWS:
weight_at_feed_adjust = IF Digestion_start > 0
THEN Chick_body_weight_at_feeding_moment_g
ELSE 0
```

```
INIT Chick_body_weight_g = 69.2
INFLOWS:
Chick_weight_gain_g = total_provision_g
OUTFLOWS:
Chick_weight_loss_before_feed_g_h = IF Period_of_digestion=0
THEN
 (((3.181*10^-3)+RANDOM(-0.928*10^-3 , 0.928*10^-3))*Chick_body_weight_g) + (0.434+RANDOM(-0.669,0.669))
ELSE 0
Chick_weight_loss_after_feed_g_h = IF Period_of_digestion= 0
THEN 0
ELSE
(((2.810*10^-3)+((RANDOM(-1.183,1.183)*10^-3)) * Chick_body_weight_at_feeding_moment_g) +
(((1.640*10^-2)+(RANDOM(-0.515,0.515)*10^-2)) * Period_of_digestion) + (1.384+RANDOM(-0.937,0.937)))
```

COMPOSED VARIABLES

Breeding schedule

```
prefledging_period = IF TIME > 80*24 THEN 1 ELSE 0
```

Foraging-allocation decisions

```
FAD1_female = IF FAD1 = 1
THEN
 IF FminCondition_above_1_bellow_0 = 0
 THEN self_feeding
 ELSE provisioning
 ELSE 0
```

```
FAD1_male = IF FAD1 = 1
THEN
 IF MminCondition_above_1_bellow_0 = 0
 THEN self_feeding
 ELSE provisioning
ELSE 0
```

```
FAD2_female = IF FAD2 = 1
THEN
 (
IF FminCondition_above_1_bellow_0 = 0
THEN self_feeding
ELSE
```

```
IF ChickCondition_good_1_poor_0 = 0
THEN provisioning
ELSE
IF FavrCondition_above_1_bellow_0 = 1
THEN provisioning
ELSE self_feeding
) ELSE 0
```

```
FAD2_male = IF FAD2 = 1
THEN
 (
IF MminCondition_above_1_bellow_0 = 0
THEN self_feeding
ELSE
IF ChickCondition_good_1_poor_0 = 0
THEN provisioning
ELSE
IF MavrCondition_above_1_bellow_0 = 1
THEN provisioning
ELSE self_feeding
)
 ELSE 0
```

```
FAD3_female = IF FAD3 = 1
THEN
 (
IF FminCondition_above_1_bellow_0 = 0
THEN self_feeding
ELSE
IF ChickCondition_good_1_poor_0 = 1
THEN
IF FavrCondition_above_1_bellow_0 = 1
THEN provisioning
ELSE self_feeding
ELSE
 IF Male_foraging_at_sea_days > 3
THEN provisioning
ELSE
IF FavrCondition_above_1_bellow_0 = 1
THEN provisioning
ELSE self_feeding
) ELSE 0
```

```
FAD3_male = IF FAD3 = 1
THEN
 (
IF MminCondition_above_1_bellow_0 = 0
THEN self_feeding
ELSE
IF ChickCondition_good_1_poor_0 = 1
THEN
IF MavrCondition_above_1_bellow_0 = 1
THEN provisioning
ELSE self_feeding
ELSE
 IF  Female_foraging_at_sea_days > 3
THEN provisioning
ELSE
IF MavrCondition_above_1_bellow_0 = 1
THEN provisioning
ELSE self_feeding
) ELSE 0
```

```
FAD4_female = IF FAD4 = 1
THEN
 ( IF FminCondition_above_1_bellow_0 = 0
 THEN self_feeding
 ELSE
  IF ChickCondition_good_1_poor_0 = 1
  THEN
   IF FavrCondition_above_1_bellow_0 = 0
   THEN self_feeding
   ELSE provisioning
  ELSE
   IF Male_foraging_at_sea_days > 3
   THEN provisioning
   ELSE
   IF FavrCondition_above_1_bellow_0 = 1
    THEN provisioning
    ELSE
    IF female_body_index > male_body_index THEN self_feeding ELSE provisioning
) ELSE 0
```

```
FAD4_male = IF FAD4 = 1
THEN
 (
 IF MminCondition_above_1_bellow_0 = 0
 THEN self_feeding
 ELSE
  IF ChickCondition_good_1_poor_0 = 1
  THEN
   IF MavrCondition_above_1_bellow_0 = 0
   THEN self_feeding
   ELSE provisioning
  ELSE
   IF  Female_foraging_at_sea_days > 3
   THEN provisioning
   ELSE
    IF MavrCondition_above_1_bellow_0 = 1
    THEN provisioning
    ELSE
    IF male_body_index > female_body_index THEN self_feeding ELSE provisioning
) ELSE 0
```

Foraging trip duration

```
FAD_female_provision_vs_self_feeding = IF FAD1 = 1 THEN FAD1_female ELSE
IF FAD2 = 1 THEN FAD2_female ELSE
IF FAD3 = 1 THEN FAD3_female ELSE
IF FAD4 = 1 THEN FAD4_female ELSE 0
```

```
FAD_male_provision_vs_self_feeding = IF FAD1 = 1 THEN FAD1_male ELSE
IF FAD2 = 1 THEN FAD2_male ELSE
IF FAD3 = 1 THEN FAD3_male ELSE
IF FAD4 = 1 THEN FAD4_male ELSE 0
```

```
generation_Female_FT_duration_days = ABS
(IF FAD_female_provision_vs_self_feeding <> 0
THEN (
 IF FAD_female_provision_vs_self_feeding = provisioning
 AND RANDOM(1,10) <=7
 THEN
 1
 ELSE
  IF FAD_female_provision_vs_self_feeding = provisioning
  AND RANDOM(1,10) > 7
 THEN
IF RANDOM(1,10) <=6 THEN 2 ELSE 3
```

```
  ELSE
   IF FAD_female_provision_vs_self_feeding = self_feeding
   THEN
IF  NORMAL(5,1.75) < 3.5 THEN 5 ELSE  NORMAL(5,1.75)
   ELSE 0
) ELSE 0)

generation_Male_FT_duration_days = ABS(IF FAD_male_provision_vs_self_feeding <> 0
THEN (
 IF FAD_male_provision_vs_self_feeding = provisioning
 AND RANDOM(1,10) <= 7
 THEN 1
 ELSE
  IF FAD_male_provision_vs_self_feeding = provisioning
  AND RANDOM(1,10) > 7
  THEN
IF RANDOM(1,10) <=6 THEN 2 ELSE 3
  ELSE
   IF FAD_male_provision_vs_self_feeding = self_feeding
   THEN
IF NORMAL(5,1.75)<3.5 THEN 5 ELSE  NORMAL(5,1.75)
   ELSE 0
) ELSE 0)

Female_FT_duration_days =
IF ROUND(generation_Female_FT_duration_days) < 1
THEN 1
ELSE ROUND(generation_Female_FT_duration_days)

Male_FT_duration_days =
IF ROUND(generation_male_FT_duration_days) < 1
THEN 1
ELSE ROUND(generation_male_FT_duration_days)
```

Nest attendance dynamics

```
Effective_Female_FT_duration_days = (IF prefledging_period=1 AND ChickCondition_good_1_poor_0 =
1 AND Female_FT_duration_days<5
THEN 5
ELSE Female_FT_duration_days)

Effective_Male_FT_duration_days = (IF prefledging_period =1 AND ChickCondition_good_1_poor_0 = 1
AND Male_FT_duration_days<5
THEN 5
ELSE Male_FT_duration_days)

Female_foraging_at_sea_days = IF (Female_foraging_at_sea_h/24) < 1
THEN 1
ELSE
ROUND(Female_foraging_at_sea_h/24)

Female_FT_duration_days_at_nest_arrival = IF TIME > 0
AND Female_nest_arrival_h > 0
THEN Female_nest_arrival_h*DT/24
ELSE 0

Female_FT_duration_days_at_nest_departure = IF TIME > 0
AND Female_nest_departure_h > 0
THEN Female_nest_departure_h*DT/24
ELSE 0

Male_foraging_at_sea_days = IF (Male_foraging_at_sea_h/24) < 1
THEN 1
ELSE
ROUND(Male_foraging_at_sea_h/24)

Male_FT_duration_days_at_nest_arrival = IF TIME > 0
AND Male_nest_arrival_h > 0
THEN Male_nest_arrival_h*DT/24
ELSE 0
```

Male_FT_duration_days_at_nest_departure = IF TIME > 0 AND Male_nest_departure_h > 0 THEN Male_nest_departure_h*DT/24 ELSE 0
Adults' mass gains at sea
Efective_female_mass_gains_at_sea = IF Reference_scenario_option = 1 THEN female_mass_gains_at_sea_grams_Reference_scenario ELSE IF Poor_FC_option = 1 THEN female_mass_gains_at_sea_grams_Poor_FC ELSE IF Very_Poor_FC_option THEN female_mass_gains_at_sea_grams_Very_Poor_FC ELSE 0
Effective_Male_mass_gains_at_sea = IF Reference_scenario_option = 1 THEN Male_mass_gains_at_sea_grams_Reference_scenario ELSE IF Poor_FC_option = 1 THEN Male_mass_gains_at_sea_grams_Poor_FC ELSE IF Very_Poor_FC_option THEN Male_mass_gains_at_sea_grams_Very_Poor_FC ELSE 0
female_mass_gains_at_sea_grams_Reference_scenario = IF Female_FT_duration_days_at_nest_departure = 1 THEN (-7.6) ELSE IF Female_FT_duration_days_at_nest_departure = 2 THEN (-13.3) ELSE IF Female_FT_duration_days_at_nest_departure = 3 THEN (27) ELSE IF Female_FT_duration_days_at_nest_departure = 4 THEN (78.3) ELSE IF Female_FT_duration_days_at_nest_departure = 5 THEN (107.9) ELSE IF Female_FT_duration_days_at_nest_departure = 6 THEN (102.6) ELSE IF Female_FT_duration_days_at_nest_departure = 7 THEN (151.6) ELSE IF Female_FT_duration_days_at_nest_departure = 8 THEN (158.7) ELSE IF Female_FT_duration_days_at_nest_departure = 9 THEN (141.1) ELSE IF Female_FT_duration_days_at_nest_departure = 10 THEN (173.3) ELSE IF Female_FT_duration_days_at_nest_departure = 11 THEN (143.5) ELSE IF Female_FT_duration_days_at_nest_departure = 12 THEN (154.7) ELSE IF Female_FT_duration_days_at_nest_departure = 13 THEN (154.7) ELSE IF Female_FT_duration_days_at_nest_departure = 14 THEN (127.9) ELSE IF Female_FT_duration_days_at_nest_departure >= 15 THEN (98.6) ELSE 0

```
female_mass_gains_at_sea_grams_Poor_FC = IF Female_FT_duration_days_at_nest_departure = 1
THEN (-28)
ELSE
IF Female_FT_duration_days_at_nest_departure = 2
THEN (-39)
ELSE
IF Female_FT_duration_days_at_nest_departure = 3
THEN (8.3)
ELSE
IF Female_FT_duration_days_at_nest_departure = 4
THEN (78.3)
ELSE
IF Female_FT_duration_days_at_nest_departure = 5
THEN (107.9)
ELSE
IF Female_FT_duration_days_at_nest_departure = 6
THEN (102.6)
ELSE
IF Female_FT_duration_days_at_nest_departure = 7
THEN (151.6)
ELSE
IF Female_FT_duration_days_at_nest_departure = 8
THEN (158.7)
ELSE
IF Female_FT_duration_days_at_nest_departure = 9
THEN (141.1)
ELSE
IF Female_FT_duration_days_at_nest_departure = 10
THEN (173.3)
ELSE
IF Female_FT_duration_days_at_nest_departure = 11
THEN (143.5)
ELSE
IF Female_FT_duration_days_at_nest_departure = 12
THEN (154.7)
ELSE
IF Female_FT_duration_days_at_nest_departure = 13
THEN (154.7)
ELSE
IF Female_FT_duration_days_at_nest_departure = 14
THEN (127.9)
ELSE
IF Female_FT_duration_days_at_nest_departure >= 15
THEN (98.6)
ELSE 0
```

```
female_mass_gains_at_sea_grams_Very_Poor_FC = IF Female_FT_duration_days_at_nest_departure = 1
THEN (-48.3)
ELSE
IF Female_FT_duration_days_at_nest_departure = 2
THEN (-64.6)
ELSE
IF Female_FT_duration_days_at_nest_departure = 3
THEN (-10.4)
ELSE
IF Female_FT_duration_days_at_nest_departure = 4
THEN (78.3)
ELSE
IF Female_FT_duration_days_at_nest_departure = 5
THEN (107.9)
ELSE
```

```
IF Female_FT_duration_days_at_nest_departure = 6
THEN (102.6)
ELSE
IF Female_FT_duration_days_at_nest_departure = 7
THEN (151.6)
ELSE
IF Female_FT_duration_days_at_nest_departure = 8
THEN (158.7)
ELSE
IF Female_FT_duration_days_at_nest_departure = 9
THEN (141.1)
ELSE
IF Female_FT_duration_days_at_nest_departure = 10
THEN (173.3)
ELSE
IF Female_FT_duration_days_at_nest_departure = 11
THEN (143.5)
ELSE
IF Female_FT_duration_days_at_nest_departure = 12
THEN (154.7)
ELSE
IF Female_FT_duration_days_at_nest_departure = 13
THEN (154.7)
ELSE
IF Female_FT_duration_days_at_nest_departure = 14
THEN (127.9)
ELSE
IF Female_FT_duration_days_at_nest_departure >= 15
THEN (98.6)
ELSE 0
```

```
Male_mass_gains_at_sea_grams_Reference_scenario = IF Male_FT_duration_days_at_nest_departure = 1
THEN (-7.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 2
THEN (-13.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 3
THEN (27)
ELSE
IF Male_FT_duration_days_at_nest_departure = 4
THEN (78.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 5
THEN (107.9)
ELSE
IF Male_FT_duration_days_at_nest_departure = 6
THEN (102.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 7
THEN (151.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 8
THEN (158.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 9
THEN (141.1)
ELSE
IF Male_FT_duration_days_at_nest_departure = 10
THEN (173.3)
ELSE
```

```
IF Male_FT_duration_days_at_nest_departure = 11
THEN (143.5)
ELSE
IF Male_FT_duration_days_at_nest_departure = 12
THEN (154.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 13
THEN (154.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 14
THEN (127.9)
ELSE
IF Male_FT_duration_days_at_nest_departure >= 15
THEN (98.6)
ELSE 0
```

```
Male_mass_gains_at_sea_grams_Poor_FC = IF Male_FT_duration_days_at_nest_departure = 1
THEN (-28)
ELSE
IF Male_FT_duration_days_at_nest_departure = 2
THEN (-39)
ELSE
IF Male_FT_duration_days_at_nest_departure = 3
THEN (8.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 4
THEN (78.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 5
THEN (107.9)
ELSE
IF Male_FT_duration_days_at_nest_departure = 6
THEN (102.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 7
THEN (151.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 8
THEN (158.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 9
THEN (141.1)
ELSE
IF Male_FT_duration_days_at_nest_departure = 10
THEN (173.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 11
THEN (143.5)
ELSE
IF Male_FT_duration_days_at_nest_departure = 12
THEN (154.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 13
THEN (154.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 14
THEN (127.9)
ELSE
IF Male_FT_duration_days_at_nest_departure >= 15
THEN (98.6)
ELSE 0
```

```
Male_mass_gains_at_sea_grams_Very_Poor_FC = IF Male_FT_duration_days_at_nest_departure = 1
THEN (-48.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 2
THEN (-64.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 3
THEN (-10.4)
ELSE
IF Male_FT_duration_days_at_nest_departure = 4
THEN (78.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 5
THEN (107.9)
ELSE
IF Male_FT_duration_days_at_nest_departure = 6
THEN (102.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 7
THEN (151.6)
ELSE
IF Male_FT_duration_days_at_nest_departure = 8
THEN (158.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 9
THEN (141.1)
ELSE
IF Male_FT_duration_days_at_nest_departure = 10
THEN (173.3)
ELSE
IF Male_FT_duration_days_at_nest_departure = 11
THEN (143.5)
ELSE
IF Male_FT_duration_days_at_nest_departure = 12
THEN (154.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 13
THEN (154.7)
ELSE
IF Male_FT_duration_days_at_nest_departure = 14
THEN (127.9)
ELSE
IF Male_FT_duration_days_at_nest_departure >= 15
THEN (98.6)
ELSE 0
```

Adults' body condition

```
FminCondition_above_1_bellow_0 = IF female_body_mass_grams <= Fminbw_grams
THEN 0
ELSE  1
```

```
FavrCondition_above_1_bellow_0 = IF TIME < guarding_period_days*24 THEN 1
ELSE
IF female_body_mass_grams >= Favrbw_grams
THEN 1
ELSE 0
```

```
female_body_index = IF TIME < guarding_period_days*24 THEN 1
ELSE
Favrbw_grams/(female_body_mass_grams)
```

```
MminCondition_above_1_bellow_0 = IF male_body_mass_grams <= Mminbw_grams
THEN 0
```

```
ELSE  1
```

```
MavrCondition_above_1_bellow_0 = IF TIME < guarding_period_days*24 THEN 1
ELSE
IF male_body_mass_grams >= Mavrbw_grams
THEN 1
ELSE 0
```

```
male_body_index = IF TIME < guarding_period_days*24 THEN 1
ELSE
Mavrbw_grams/(male_body_mass_grams)
```

Meal size

```
Female_Meal_size_g_per_FT = IF Female_FT_duration_days_at_nest_arrival=1
THEN 45
ELSE
IF Female_FT_duration_days_at_nest_arrival=2
THEN 94
ELSE
IF Female_FT_duration_days_at_nest_arrival=3
THEN 126
ELSE
IF Female_FT_duration_days_at_nest_arrival=4
THEN 128
ELSE
IF Female_FT_duration_days_at_nest_arrival=5
THEN 125
ELSE
IF Female_FT_duration_days_at_nest_arrival=6
THEN 90
ELSE
IF Female_FT_duration_days_at_nest_arrival=7
THEN 112
ELSE
IF Female_FT_duration_days_at_nest_arrival=8
THEN 128
ELSE
IF Female_FT_duration_days_at_nest_arrival >= 9
THEN 180
ELSE 0
```

```
Male_Meal_size_g_per_FT = IF Male_FT_duration_days_at_nest_arrival=1
THEN 45
ELSE
IF Male_FT_duration_days_at_nest_arrival=2
THEN 94
ELSE
IF Male_FT_duration_days_at_nest_arrival=3
THEN 126
ELSE
IF Male_FT_duration_days_at_nest_arrival=4
THEN 128
ELSE
IF Male_FT_duration_days_at_nest_arrival=5
THEN 125
ELSE
IF Male_FT_duration_days_at_nest_arrival=6
THEN 90
ELSE
IF Male_FT_duration_days_at_nest_arrival=7
THEN 112
ELSE
```

IF Male_FT_duration_days_at_nest_arrival=8
THEN 128
ELSE
IF Male_FT_duration_days_at_nest_arrival >= 9
THEN 180
ELSE 0

Female_food_delivery_g_per_FT = IF TIME <guarding_period_days*24 THEN Female_Meal_size_g_per_FT ELSE Female_Meal_size_g_per_FT

Male_food_delivery_g_per_FT = IF TIME <guarding_period_days*24 THEN Male_Meal_size_g_per_FT*0 ELSE Male_Meal_size_g_per_FT

total_provision_g = Female_food_delivery_g_per_FT+Male_food_delivery_g_per_FT

Chick body condition

ChickCondition_good_1_poor_0 = IF TIME < guarding_period_days*24 THEN 0 ELSE (IF Chick_body_weight_at_feeding_moment_g > optimal_growth THEN 1 ELSE 0)

optimal growth = (26.31+33.36*days_after_chick_hatching-0.26*(days_after_chick_hatching^2))

CONSTANTS

Breeding Schedule

guarding_period_days = 5

Foraging-allocation decisions

provisioning = 1

self_feeding = 2

Adults' body condition

Fminbw_grams = 0.88*Favrbw_grams

Favrbw_grams = HISTORY(female_body_mass_grams,0)

Fmaxbw_grams = 1.12*Favrbw_grams

Mminbw_grams = 0.88*Mavrbw_grams

Mavrbw_grams = HISTORY(male_body_mass_grams,0)

Mmaxbw_grams = 1.12*Mavrbw_grams

SWITCHERS

FAD1 = 0

FAD2 = 0

FAD3 = 0

FAD4 = 0

Poor_FC_option = 0

Reference_scenario_option = 0

Very_Poor_FC_option = 0

OTHER VARIABLES

Nest attendance dynamics

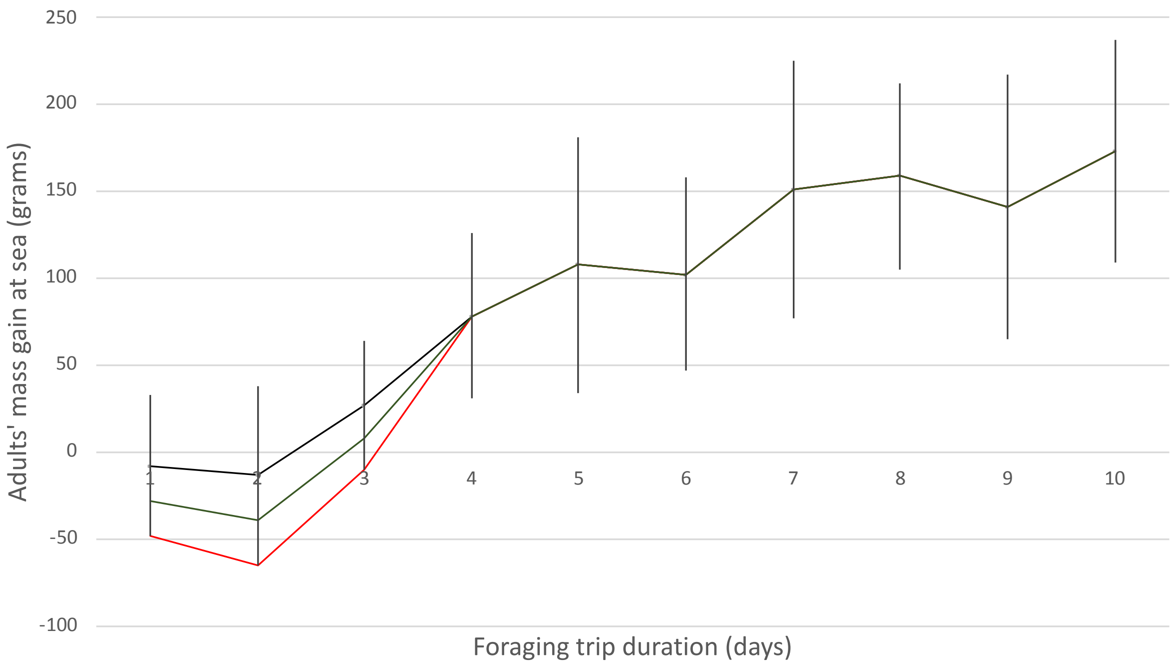
Counter_Female_time_at_sea_h = COUNTER(0, Female_foraging_at_sea_h)

Counter_Male_time_at_sea_h = COUNTER (0, Male_foraging_at_sea_h)

Chick body condition

days_after_chick_hatching = INT(TIME/24)

Appendix J - Variations in adults' body mass in relation to foraging trip duration, based on incubation shifts of Cory's shearwaters breeding at Selvagem Grande in 2006 (black line; hereinafter, reference scenario) (obtained from Ramos et al. 2009; data pooled for males and females; n = 173 foraging trips). Mass gains at sea are presented as mean ± standard deviation. Two additional environmental scenarios were set, which consider: a sharp decrease in local foraging conditions (≤ 3 foraging trip days) based on the lower limit of the variation around the mean (red line; hereinafter, very poor foraging conditions), and an intermediate decrease given the central value between the lower limit and the average mass gains in the reference scenario (green line; hereinafter, poor foraging conditions).



References

Ramos JA, Granadeiro JP, Phillips RA, Catry P (2009). Flight morphology and foraging behavior of male and female Cory's shearwaters. Condor, 111(3): 424–432.

Appendix K - Holm pairwise pos-hoc multiple comparisons and statistical significance (p-value) (* p<0.05; ** p<0.01; *** p<0.001; **.** p<0.1) for females' body condition, chick feeding frequency and chick growth rate among all foraging-allocation decisions per environmental scenario considered (Reference scenario, Poor Foraging Conditions and Very Poor Foraging Conditions). Foraging allocation decisions (FADs) assume sequential adaptive compromises among family members: FAD 1 - provisioning is determined by the adults' critical body mass threshold for reproduction; FAD 2 - based on FAD 1, provisioning is determined by short-term variations in chick's nutritional status; FAD 3 - based on FAD 2, provisioning is determined by the partner's allocation decision; FAD 4 - based on FAD 3, provisioning is determined by the partner's body condition.

	Female' body condition				Chick' feeding frequency				Chick' daily growth rate			
Reference Scenario	FAD 1	FAD 2	FAD 3	FAD 4	FAD 1	FAD 2	FAD 3	FAD 4	FAD 1	FAD 2	FAD 3	FAD 4
FAD 1		119.9 (8.8e-13 ***)	239.8 (< 2e-16 ***)	243.0 (< 2e-16 ***)		-124.3 (1.6e-13 ***)	-110.0 (8.0e-11 ***)	-20.1 (0.4346)		118.4 (2.8e-12 ***)	21.9 (0.3820)	-3.2 (0.8476)
FAD 2			119.9 (8.8e-13 ***)	123.1 (2.7e-13 ***)			14.3 (0.4346)	104.2 (7.0e-10 ***)			-96.5 (1.7e-08 ***)	-121.6 (8.1e-13 ***)
FAD 3				3.2 (0.8452)				89.9 (1.1e-07 ***)				-25.0 (0.3820)
FAD 4												

	Female' body condition				Feeding frequency			
Poor Foraging Conditions	FAD 1	FAD 2	FAD 3	FAD 4	FAD 1	FAD 2	FAD 3	FAD 4
FAD 1		11.1 (0.4975)	230.1 (< 2e-16 ***)	122.6 (3.3e-13 ***)		6.2 (1.0000)	-1.0 (1.0000)	132.5 (3.0e-15 ***)
FAD 2			218.9 (< 2e-16 ***)	111.5 (3.5e-11 ***)			-7.3 (1.0000)	126.2 (5.0e-14 ***)
FAD 3				-107.4 (1.3e-10 ***)				133.5 (2.1e-15 ***)
FAD 4								

	Female' body condition				Feeding frequency			
Very Poor Foraging Conditions	FAD 1	FAD 2	FAD 3	FAD 4	FAD 1	FAD 2	FAD 3	FAD 4
FAD 1		6.6 (0.68598)	184.6 (< 2e-16 ***)	72.2 (3.4e-05 ***)		-10.4 (1.0000)	-1.9 (1.0000)	47.9 (0.0137 *)
FAD 2			177.9 (< 2e-16 ***)	65.5 (0.00013 ***)			8.5 (1.0000)	58.4 (0.0022 **)
FAD 3				-112.4 (3.2e-11 ***)				49.9 (0.0116 *)
FAD 4								

Chapter 4

Appendix M – Model conceptualization: Yellow-legged gull population dynamics.

A) PURPOSE

The model was designed to simulate the Yellow-legged Gull population dynamics from the Berlenga Island (Portugal), based on the species reproductive biology and mechanisms regulating their intrinsic dynamics. In order to incorporate natural individual variability in the model parameterization, the demographic parameters influencing the population dynamics were generated as random values within realistic limits (i.e. minimum and maximum values) described in bibliographic sources (Appendix L).

B) STRUCTURE AND FUNCTIONING

1. CONCEPTUAL DIAGRAM

2. PRE AND POST DUMPS SCHEDULE

3. BREEDING CYCLE

1. CONCEPTUAL DIAGRAM

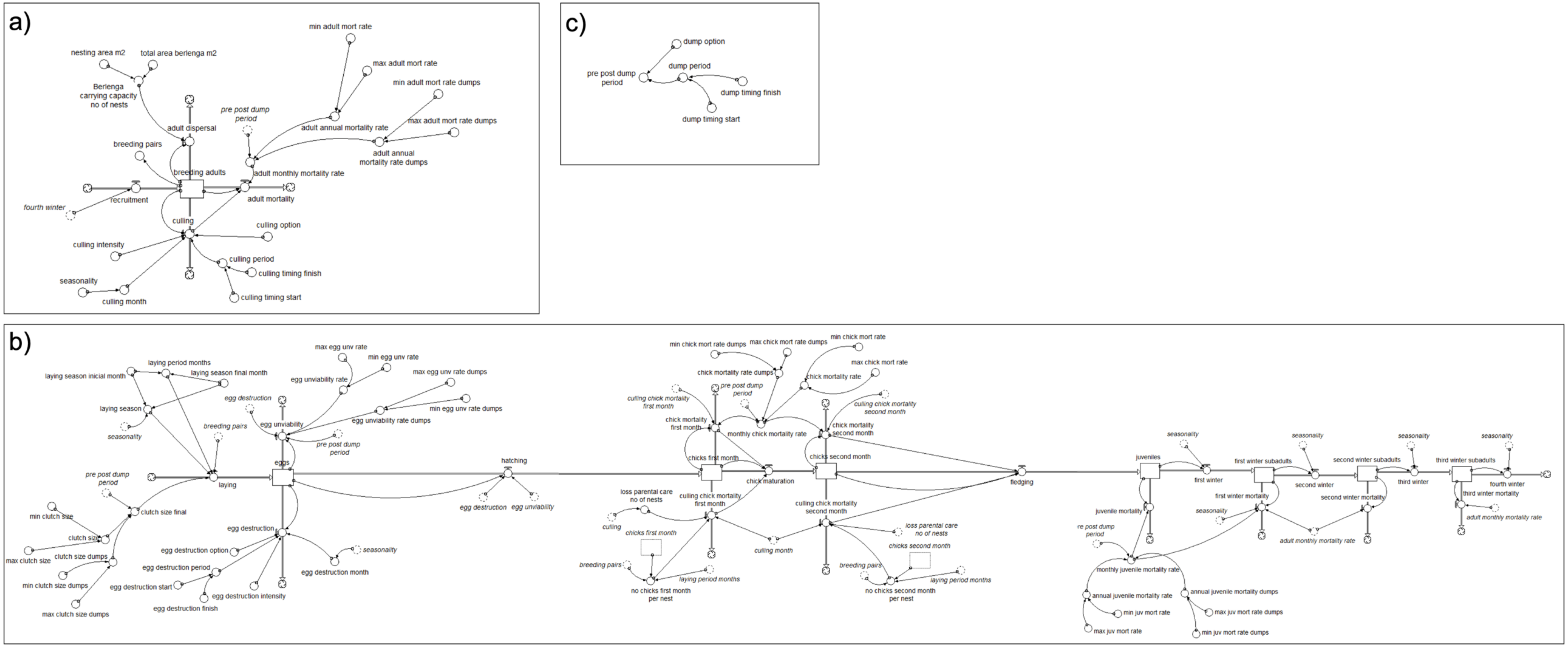


Figure 1. Conceptual diagram of the model to simulate the Yellow-legged Gull population dynamics based on the species reproductive biology and the mechanisms regulating their intrinsic dynamics. The model is composed of different sub-models and their interactions: (a) population dynamics of breeding adults; (b) reproduction and the population dynamics of non-breeding individuals, assuming eggs, chicks (of first and second month), juveniles, and subadults (of first, second and third winter); (c) the periods of either availability or absence of operating open-air dumps. Rectangles represent state variables; parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows.

2. PRE AND POST DUMPS SCHEDULE

The period when open-air dumps are active.
Modelling elements:

- *pre post dump period* (Figure 1, Appendix N – “Composed Variables”)

2.1. Dump period

The period when open-air dumps are active througtout simulation.
Modelling elements:

- *Dump option* (Figure 1, Appendix N – “Switchers”)
- *Dump period* (Figure 1, Appendix N – “Composed Variables”)
- *Dump timing start* (Figure 1, Appendix N – “Constants”)
- *Dump timing finish* (Figure 1, Appendix N – “Constants”)

3. BREEDING CYCLE

To model the complete life cycle of the Yellow-legged Gull, five life stages were considered: eggs, chicks, juveniles, subadults and breeding adults. Chicks were divided into first and second-month chicks, and subadults were divided into first, second and third-winter subadults. Therefore, a total of 8 state variables were considered, representing the number of individuals in each demographic stage. The Yellow-legged gull breeding season was defined from April to July, in which April and May correspond to the laying season (Rainha 1996). Eggs hatched after one month (i.e. incubation stage), in May or June, depending on the month they were laid. After hatching, chicks fledged to juveniles after two months, being July the last month of chick maturation. Subadults transit between life stages (first to second and to third winter) in December, and reach sexual maturity at the age of four years, assuming the average described for the species (Coulson et al. 1982; Morais et al. 1998; Serra et al. 2016). At this stage, birds enter the breeding population.
Since the model runs on a monthly basis, every rate coming from original measurements other than a month was standardized following the equation (Chaves et al. 2000):

$$Monthly\,rate = (1 + rate)^{\left(\frac{1}{n}\right)} - 1$$

STATE VARIABLES:

3.1. BREEDING ADULTS (*breeding adults*) (Figure 1, Appendix N – “Difference and Process Equations”)
3.2. EGGS (*eggs*) (Figure 1, Appendix N – “Difference and Process Equations”)
3.3. CHICKS (*chicks first month; chicks second month*) (Figure 1, Appendix N – “Difference and Process Equations”)
3.4. JUVENILES *(juveniles)* (Figure 1, Appendix N – “Difference and Process Equations”)
3.5. SUBADULTS (*first winter subadults; second winter subadults; third winter subadults*) (Figure 1, Appendix N – “Difference and Process Equations”)

3.1. BREEDING ADULTS

Adult birds that reproduce every year. The breeding population dynamics result from the balance between individuals reaching the age of sexual maturity (third-winter subadults that enter the breeding population) and the natural mortality of adults. Space was considered a limiting demographic factor and therefore when the carrying capacity of the island is exceeded, individuals are forced to leave the area (dispersal). In culling periods, adult mortality is also aggravated by the direct consequences of management actions. The initial number of breeding adults was defined as 4640 (2320 males and 2320 females), according to census performed in 1978 (SPEA 2016). Breeding adults are converted in number of breeding pairs through the variable *breeding pairs* (Appendix N – "Composed Variables").

PROCESSES:

3.1.1. ADULT RECRUITMENT

recruitment (Figure 1, Appendix N – "Process Equations")

3.1.2. ADULT NATURAL MORTALITY

adult mortality (Figure 1, Appendix N – "Process Equations")

3.1.3. ADULT DISPERSAL (CARRYING CAPACITY)

adult dispersal (Figure 1, Appendix N – "Process Equations")

3.1.4 ADULT CULLING

culling (Figure 1, Appendix N – "Process Equations")

3.1.1. ADULT RECRUITMENT

Subadults that reach the age of first breeding.

Modelling elements:

- *fourth winter* (Figure 1, Appendix N – "Process Equations")

3.1.2. ADULT NATURAL MORTALITY

Adult birds that die due to natural causes.

Modelling elements

- *breeding adults* (Figure 1, Appendix N – "Difference and Process Equations")
- *adult monthly mortality rate* (Figure 1, Appendix N – "Composed Variables")

3.1.2.1. Adult natural mortality rate

The adult natural mortality was estimated from annual survival rates, and determines the proportion of individuals that die due to natural causes throughout time, ranging between 0.077 and 0.11 before dumps closure (Migot 1992; Lebreton et al. 1995) and between 0.16 and 0.23 after dumps closure (Juez et al. 2015). Since this parameter was obtained from annual estimates, rates were monthly adjusted.

Modelling elements

- *min adult mort rate* (Figure 1, Appendix L and Appendix N – "Constants")
- *max adult mort rate* (Figure 1, Appendix L and Appendix N – "Constants")
- *min adult mort rate dumps* (Figure 1, Appendix L and Appendix N – "Constants")
- *max adult mort rate dumps* (Figure 1, Appendix L and Appendix N – "Constants")
- *annual adult mortality rate* (Figure 1, Appendix N – "Random Variables")
- *annual adult mortality rate dumps* (Figure 1, Appendix N – "Random Variables")
- *pre post dump closure period* (Figure 1, Appendix N – "Composed Variables")

3.1.3. ADULT DISPERSAL

Adult birds that leave the breeding population due to space constraints associated with the Berlenga carrying capacity.
Modelling elements:

- *breeding adults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *culling* (Figure 1, Appendix N – “Process Equations”)
- Berlenga carrying capacity no of nests (Figure 1, Appendix N – “Composed Variables”)

3.1.3.1. Berlenga carrying capacity

The island carrying capacity was assumed as the maximum possible number of nests on the island, considering the average nesting area per breeding pair (Luís 1982), and the total area of the Berlenga (Amado et al. 2007).
Modelling elements:

- *nesting area m2* (Figure 1, Appendix L and Appendix N – “Constants”)
- *total area berlenga m2* (Figure 1, Appendix L and Appendix N – “Constants”)

3.1.4. ADULT CULLING

Adult birds that die from culling.
Modelling elements:

- *breeding adults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *culling option* (Figure 1, Appendix N – “Switchers”)
- *culling intensity* (Figure 1, Appendix L and Appendix N – “Constants”)
- *culling period* (Figure 1, Appendix N – “Composed Variables”)
- *culling month* (Figure 1, Appendix N – “Composed Variables”)

3.1.4.1. Culling intensity

The proportion of breeding adults culled annually, defined as 0.62 through calibration procedure.

3.1.4.2. Culling period

The period of culling.
Modelling elements:

- *culling timing finish* (Figure 1, Appendix N – “Constants”)
- *culling timing start* (Figure 1, Appendix N – “Constants”)

3.1.4.3. Culling month

The month of the year when culling occurs (i.e. June).

3.2. EGGS

Eggs laid by females and incubated during one month. The dynamics of eggs result from the balance between laid and unviable eggs. In years when control programs are active, eggs were broken and lost. The initial number of eggs was considered 0, as the breeding season was inactive in the beginning of the simulation.

PROCESSES:

3.2.1. LAYING

laying (Figure 1, Appendix N – “Process Equations”)

3.2.2. EGG NATURAL INVIAIBILITY

Egg unviability (Figure 1, Appendix N – “Process Equations”)

3.2.3. EGG DESTRUCTION MANAGEMENT

egg destruction (Figure 1, Appendix N – “Process Equations”)

3.2.1. LAYING

Nesting attempts leading up to egg stage. Eggs are generated taking into account the number of breeding pairs and clutch size per pair.

Modelling elements:

- *breeding pairs* (Figure 1, Appendix N – “Composed variables”)
- *laying season* (Figure 1, Appendix N – “Composed variables”)
- *laying period months* (Figure 1, Appendix N – “Composed Variables”)
- *clutch size final* (Figure 1, Appendix N – “Composed variables”)

3.2.1.1. Laying season

The laying season occurs during two months, in April and May (Rainha 1996).

Modelling elements:

- *laying season initial month* (Figure 1, Appendix N – “Constants”)
- *laying season final month* (Figure 1, Appendix N – “Constants”)
- *laying period months* (Figure 1, Appendix N – “Composed Variables”)
- *seasonality* (Figure 1, Appendix N – “Other Variables”)

3.2.1.2. Clutch size

Number of eggs laid per female, ranging between 2.63 and 2.90 eggs before dumps closure (Pons and Migot 1995; Steigerwald et al. 2015) and between 2.37 and 2.66 eggs after dumps closure (Pons and Migot 1995; Steigerwald et al. 2015).

Modelling elements:

- *min clutch size* (Figure 1, Appendix L and Appendix N – “Constants”)
- *max clutch size* (Figure 1, Appendix L and Appendix N – “Constants”)
- *min clutch size dumps* (Figure 1, Appendix L and Appendix N – “Constants”)
- *max clutch size dumps* (Figure 1, Appendix L and Appendix N – “Constants”)
- *clutch size* (Figure 1, Appendix N – “Random Variables”)
- *clutch size dumps* (Figure 1, Appendix N – “Random Variables”)
- *pre post dump closure period* (Figure 1, Appendix N – “Composed Variables”)

3.2.2. EGG UNVIABILTY

Unviable eggs due to natural causes.

Modelling elements:

- *eggs* (Figure 1, Appendix N – “Difference and Process Equations”)

- *egg destruction* (Figure 1, Appendix N – “Process Equations”)
- *egg unviability rate* (Figure 1, Appendix N – “Random Variables”)
- *egg unviability rate dumps* (Figure 1, Appendix N – “Random Variables”)
- *pre post dump closure period* (Figure 1, Appendix N – “Composed Variables”)

3.2.2.1. Egg unviability rate

Egg unviability rate was estimated from hatching success, and determines the proportion of eggs that don’t hatch due to natural causes, ranging between 0.172 and 0.292 before dumps closure (Pons 1992; Duhem et al. 2002) and between 0.372 and 0.439 after dumps closure (Pons 1992; Duhem et al. 2002).

Modelling elements:

- *min egg unv rate* (Figure 1, Appendix L and Appendix N – “Constants”)
- *max egg unv rate* (Figure 1, Appendix L and Appendix N – “Constants”)
- *min egg unv rate dumps* (Figure 1, Appendix L and Appendix N – “Constants”)
- *max egg unv rate dumps* (Figure 1, Appendix L and Appendix N – “Constants”)

3.2.3. EGG DESTRUCTION MANAGEMENT

Eggs lost due to egg destruction campaigns.

Modelling elements:

- *eggs* (Figure 1, Appendix N – “Difference and Process Equations”)
- *egg destruction option* (Figure 1, Appendix N – “Switchers”)
- *egg destruction intensity* (Figure 1, Appendix L and Appendix N – “Constants”)
- *egg destruction period* (Figure 1, Appendix N – “Composed Variables”)
- *egg destruction month* (Figure 1, Appendix N – “Composed Variables”)

3.2.3.1. Egg destruction intensity

The proportion of eggs destroyed annually, defined as 0.42 through calibration procedure.

3.2.3.2. Egg destruction period

The period of egg destruction management actions.

Modelling elements:

- *egg destruction start* (Figure 1, Appendix N – “Constants”)
- *egg destruction finish* (Figure 1, Appendix N – “Constants”)

3.2.3.3. Management month

The month of the year when egg destruction occurs (i.e. June and July).

3.3. CHICKS

Nestling birds. Chicks stay at this phase for two months before turning into juveniles when they gain the ability to flight. The dynamics of chicks result from the balance between hatched eggs and natural mortality of chicks. When the culling of adult birds occurs, chicks die due to loss of parental care. The initial number of chicks was considered 0, as breeding season was inactive at the beginning of the simulation.

PROCESSES:

3.3.1. HATCHING

hatching (Figure 1, Appendix N – “Process Equations”)

3.3.2. CHICK MATURATION

chick maturation (Figure 1, Appendix N – “Process Equations”)

3.3.3. CHICK NATURAL MORTALITY

chick mortality first month (Figure 1, Appendix N – “Process Equations”)
chick mortality second month (Figure 1, Appendix N – “Process Equations”)

3.3.4. CHICK MORTALITY CULLING

culling chick mortality first month (Figure 1, Appendix N – “Process Equations”)
culling chick mortality second month (Figure 1, Appendix N – “Process Equations”)

3.3.1. HATCHING

Successfully emancipated chicks.
Modelling elements:

- *eggs* (Figure 1, Appendix N – “Difference and Process Equations”)
- *egg unviability* (Figure 1, Appendix N – “Process Equations”)
- *egg destruction* (Figure 1, Appendix N – “Process Equations”)

3.3.2. CHICK MATURATION

Chicks that survive in the first month of life and transit into chicks of second month.
Modelling elements:

- *chick first month* (Figure 1, Appendix N – “Difference and Process Equations”)
- *chick mortality first month* (Figure 1, Appendix N – “Process Equations”)
- *culling chick mortality first month* (Figure 1, Appendix N – “Process Equations”)

3.3.3. CHICK NATURAL MORTALITY

Chicks that die due to natural causes.
Modelling elements:

- *chicks first month* (Figure 1, Appendix N – “Difference and Process Equations”)
- *chicks second month* (Figure 1, Appendix N – “Difference and Process Equations”)
- *monthly chick mortality rate* (Figure 1, Appendix N – “Composed Variables”)

3.3.3.1. Monthly chick mortality rate

Chick mortality rate was estimated from fledging success rates, and determines the proportion of chicks that die before reaching the juvenile phase, ranging between 0.526 and 0.548 before dumps closure (Oro et al. 1995; Duhem et al. 2002) and between 0.778 and 0.866 after dumps closure (Oro et

al. 1995; Duhem et al. 2002). Since this parameter was obtained from population estimates based on complete reproductive seasons, rates were monthly adjusted.
Modelling elements:

- *min chick mort rate* (Figure 1, Appendix L and Appendix N – “Constants”)
- *max chick mort rate* (Figure 1, Appendix L and Appendix N – “Constants”)
- *min chick mort rate dumps* (Figure 1, Appendix L and Appendix N – “Constants”)
- *max chick mort rate dumps* (Figure 1, Appendix L and Appendix N – “Constants”)
- *chick mortality rate* (Figure 1, Appendix N – “Random Variables”)
- *chick mortality rate dumps* (Figure 1, Appendix N – “Random Variables”)
- *pre post dump closure period* (Figure 1, Appendix N – “Composed Variables”)

3.3.4. CHICK MORTALITY CULLING

Chicks that die because breeding adults are culled and parental care is lost.
Modelling elements:

- *Culling month* (Figure 1, Appendix N – “Composed Variables”)
- *No chicks first month per nest* (Figure 1, Appendix N – “Composed Variables”)
- *No chicks second month per nest* (Figure 1, Appendix N – “Composed Variables”)
- *Loss parental care no of nests* (Figure 1, Appendix N – “Composed Variables”)

3.3.4.1. Chicks per nest

Average number of chicks (first and second month) per nest per laying month.
Modelling elements:

- *chicks first month* (Figure 1, Appendix N – “Difference and Process Equations”)
- *chicks second month* (Figure 1, Appendix N – “Difference and Process Equations”)
- *breeding pairs* (Figure 1, Appendix N – “Composed Variables”)
- *laying period months* (Figure 1, Appendix N – “Composed Variables”)

3.3.4.2. Parental care loss

Number of nests that lose parental care due to culling of breeding birds.
Modelling elements:

- *culling* (Figure 1, Appendix N – “Process Equations”)

3.4. JUVENILES

Flying birds with juvenile plumage. The dynamics of juveniles result from the balance between successfully fledged chicks and the natural mortality of juveniles. The initial number of juveniles was considered 0 since the breeding season was inactive in the beginning of the simulation.

PROCESSES

3.4.1. CHICK FLEDGING

fledging (Figure 1, Appendix N – “Process Equations”)

3.4.2. JUVENILE NATURAL MORTALITY

juvenile mortality (Figure 1, Appendix N – “Process Equations”)

3.4.1. CHICK FLEDGING

Chicks that survive in the first two months of life and survive up to independence.
Modelling elements:

- *chicks second month* (Figure 1, Appendix N – "Difference and Process Equations")
- *chick mortality second month* (Figure 1, Appendix N – "Process Equations")
- *culling chick mortality second month* (Figure 1, Appendix N – "Process Equations")

3.4.2. JUVENILE NATURAL MORTALITY

Juvenile birds that die of natural causes.
Modelling elements:

- *juveniles* (Figure 1, Appendix N – "Difference and Process Equations")
- *monthly juvenile mortality rate* (Figure 1, Appendix N – "Composed Variables")

3.4.2.1. Monthly juvenile natural mortality

Juvenile mortality rate was estimated from survival rates, and determines the proportion of juveniles that die before reaching subadults of first winter, ranging between 0.16 and 0.33 before dumps closure (Chabrzyk and Coulson 1976) and between 0.47 and 0.72 after dumps closure (Juez et al. 2015).
Modelling elements:

- *max juv mort rate* (Figure 1, Appendix L and Appendix N – "Constants")
- *min juv mort rate* (Figure 1, Appendix L and Appendix N – "Constants")
- *max juv mort rate dumps* (Figure 1, Appendix L and Appendix N – "Constants")
- *min juv mort rate dumps* (Figure 1, Appendix L and Appendix N – "Constants")
- *annual juvenile mortality rate* (Figure 1, Appendix N – "Random Variables")
- *annual juvenile mortality rate dumps* (Figure 1, Appendix N – "Random Variables")
- *pre post dump closure period* (Figure 1, Appendix N – "Composed Variables")

3.5. SUBADULTS

After the juvenile stage, individuals transit to subadults where they remain for 3 years, not affecting directly the breeding population until maturation is completed. Subadults transit between life stages (first to second and to third winter) in December, and reach sexual maturity at the age of four years, assuming the average described for the species (Coulson et al. 1982; Morais et al. 1998; Serra et al. 2016). The dynamics of subadults result from the balance between successfully matured juveniles and natural mortality of subadults. The initial number of third-winter subadults was defined based on the number of new birds that entered the breeding population in 1979 (number of breeding birds in 1979 - number of breeding birds in 1978), and the survival rate of adult birds was used to estimate their expectable abundances in 1978. Likewise, the number of second and first-winter subadults was estimated using the respective survival rates (adult annual mortality rate) for the reverse calculations of their abundances in 1978.

PROCESSES

3.5.1. NATURAL MORTALITY

first winter mortality (Figure 1, Appendix N – "Process Equations")

second winter mortality (Figure 1, Appendix N – “Process Equations”)
third winter mortality (Figure 1, Appendix N – “Process Equations”)
3.5.2. YEARLY MATURATION
first winter (Figure 1, Appendix N – “Process Equations”)
second winter (Figure 1, Appendix N – “Process Equations”)
third winter (Figure 1, Appendix N – “Process Equations”)
fourth winter (Figure 1, Appendix N – “Process Equations”)

3.5.1. NATURAL MORTALITY

Subadults that die from natural causes.
Modelling elements:

- *juveniles* (Figure 1, Appendix N – “Difference and Process Equations”)
- *first winter subadults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *second winter subadults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *third winter subadults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *monthly juvenile mortality rate* (Figure 1, Appendix N – “Composed Variables”)
- *monthly adult mortality rate* (Figure 1, Appendix N – “Composed Variables”)
- *seasonality* (Figure 1, Appendix N – “Other Variables”)

3.5.1.1. Monthly juvenile mortality rate / monthly adult mortality rate

The mortality of subadults of first winter was based in the survival of juveniles until they reach one year of life (in April of the following year) (see 3.4.2.1. ‘Monthly juvenile natural mortality’). Since these birds remain as subadults of first winter until December, after April they start being under the mortality rate of birds older than 1 year (see 3.1.2.1. ‘Adult natural mortality rate’).

3.5.2. YEARLY MATURATION

Subadults that mature yearly. Subadults transit between life stages (first to second and to third winter) in December.
Modelling elements:

- *juveniles* (Figure 1, Appendix N – “Difference and Process Equations”)
- *first winter subadults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *second winter subadults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *third winter subadults* (Figure 1, Appendix N – “Difference and Process Equations”)
- *seasonality* (Figure 1, Appendix N – “Other Variables”)

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Appendix N - Specification of all mathematic equations included in the model.

DIFFERENCE EQUATIONS
breeding_adults(t) = breeding_adults(t - dt) + (recruitment - adult_mortality - culling - adult_dispersal) * dt
eggs(t) = eggs(t - dt) + (laying - hatching - egg_destruction - egg_unviability) * dt
chicks_first_month(t) = chicks_first_month(t - dt) + (hatching - chick_mortality_first_month - chick_maturation - culling_chick_mortality_first_month) * dt
chicks_second_month(t) = chicks_second_month(t - dt) + (chick_maturation - fledging - chick_mortality_second_month - culling_chick_mortality_second_month) * dt
juveniles(t) = juveniles(t - dt) + (fledging - first_winter - juvenile_mortality) * dt
first_winter_subadults(t) = first_winter_subadults(t - dt) + (first_winter - second_winter - first_winter_mortality) * dt
second_winter_subadults(t) = second_winter_subadults(t - dt) + (second_winter - third_winter - second_winter_mortality) * dt
third_winter_subadults(t) = third_winter_subadults(t - dt) + (third_winter - third_winter_mortality - fourth_winter) * dt
PROCESS EQUATIONS
INIT breeding_adults = 4640 INFLOWS: recruitment = fourth_winter OUTFLOWS: adult_mortality = (breeding_adults-culling)*adult_monthly_mortality_rate culling = IF culling_month=1 AND culling_option=1 AND culling_period=1 THEN breeding_adults*culling_intensity ELSE 0 adult_dispersal = IF breeding_adults>Berlenga__carrying_capacity__no_of_nests THEN breeding_adults-Berlenga__carrying_capacity__no_of_nests ELSE 0
INIT eggs = 0 INFLOWS: laying = IF((laying_season=1)AND(breeding_pairs>0)) THEN((breeding_pairs*clutch_size_final)/laying_period_months) ELSE(0) OUTFLOWS: hatching = eggs-(egg_unviability+egg_destruction) egg_destruction = IF egg_destruction_month=1 AND egg_destruction_option=1 AND egg_destruction_period =1 THEN eggs*egg_destruction_intensity ELSE 0 egg_unviability = IF pre_post_dump___period=1 THEN (eggs-egg_destruction)*egg_unviability_rate_dumps ELSE (eggs-egg_destruction)*egg_unviability_rate
INIT chicks_first_month = 0 INFLOWS: hatching = eggs-(egg_unviability+egg_destruction) OUTFLOWS: chick_mortality_first_month = (chicks_first_month-culling_chick_mortality_first_month)*monthly_chick_mortality_rate chick_maturation = chicks_first_month-(chick_mortality_first_month+culling_chick_mortality_first_month) culling_chick_mortality_first_month = IF culling_month=1 THEN no_chicks_first_month_per_nest*loss_parental_care__no_of_nests ELSE 0
INIT chicks_second_month = 0 INFLOWS: chick_maturation = chicks_first_month-(chick_mortality_first_month+culling_chick_mortality_first_month) OUTFLOWS: fledging = chicks_second_month-(chick_mortality_second_month+culling_chick_mortality_second_month) chick_mortality_second_month = (chicks_second_month-culling_chick_mortality_second_month)*monthly_chick_mortality_rate

culling_chick_mortality_second_month = IF culling_month=1 THEN no_chicks_second_month__per_nest*loss_parental_care__no_of_nests ELSE 0

INIT juveniles = 0
INFLOWS:
fledging = chicks_second_month-(chick_mortality_second_month+culling_chick_mortality_second_month)
OUTFLOWS:
first_winter = IF(seasonality=11) THEN(juveniles) ELSE(0)
juvenile_mortality = juveniles*monthly_juvenile_mortality_rate

INIT first_winter_subadults = 1154
INFLOWS:
first_winter = IF(seasonality=11) THEN(juveniles) ELSE(0)
OUTFLOWS:
second_winter = IF(seasonality=11) THEN(first_winter_subadults) ELSE(0)
first_winter_mortality = IF seasonality = 12 OR seasonality < 5 THEN first_winter_subadults*monthly_juvenile_mortality_rate ELSE first_winter_subadults*adult_monthly_mortality_rate

INIT second_winter_subadults = 1046
INFLOWS:
second_winter = IF(seasonality=11) THEN(first_winter_subadults) ELSE(0)
OUTFLOWS:
third_winter = IF(seasonality=11) THEN(second_winter_subadults) ELSE(0)
second_winter_mortality = second_winter_subadults*adult_monthly_mortality_rate

INIT third_winter_subadults = 948
INFLOWS:
third_winter = IF(seasonality=11) THEN(second_winter_subadults) ELSE(0)
OUTFLOWS:
third_winter_mortality = third_winter_subadults*adult_monthly_mortality_rate
fourth_winter = IF seasonality = 11 THEN third_winter_subadults ELSE 0

COMPOSED VARIABLES

adult_monthly_mortality_rate = IF pre_post_dump___period =1 THEN ((1+adult_annual_mortality_rate_dumps)^(1/12))-1 ELSE ((1+adult_annual_mortality_rate)^(1/12))-1

Berlenga__carrying_capacity__no_of_nests = nesting_area_m2*total_area_berlenga_m2

breeding_pairs = breeding_adults/2

clutch_size_final = IF pre_post_dump___period=1 THEN clutch_size_dumps ELSE clutch_size

culling_month = IF seasonality = 6 THEN 1 ELSE 0

culling_period = IF (TIME>=culling_timing_start AND TIME <=culling_timing_finish) THEN 1 ELSE 0

dump_period = IF TIME>=dump_timing_start AND TIME<=dump_timing_finish THEN 1 ELSE 0

egg_destruction_month = IF seasonality= 4 OR seasonality = 5 THEN 1 ELSE 0

egg_destruction_period = IF TIME>=egg_destruction_start AND TIME<=egg_destruction_finish THEN 1 ELSE 0

laying_period_months = laying_season_final_month-laying_season_inicial_month+1

laying_season = IF((seasonality>=laying_season_inicial_month) AND(seasonality<=laying_season_final_month)) THEN(1) ELSE(0)

loss_parental_care__no_of_nests = culling/2

monthly_chick_mortality_rate = IF pre_post_dump___period=1 THEN ((1+chick_mortality_rate_dumps)^(1/2))-1 ELSE ((1+chick_mortality_rate)^(1/2))-1

monthly_juvenile_mortality_rate = IF pre_post_dump___period= 1 THEN ((1+annual_juvenile_mortality_dumps)^(1/12))-1 ELSE ((1+annual_juvenile_mortality_rate)^(1/12))-1

no_chicks_first_month_per_nest = chicks_first_month/(breeding_pairs/laying_period_months) no_chicks_second_month__per_nest = chicks_second_month/(breeding_pairs/laying_period_months)

pre_post_dump___period = IF dump_option = 1 AND dump_period = 1 THEN 1 ELSE 0

RANDOM VARIABLES

adult_annual_mortality_rate = RANDOM(min_adult_mort_rate,max_adult_mort_rate)

adult_annual_mortality_rate_dumps = RANDOM(min_adult_mort_rate_dumps, max_adult_mort_rate_dumps)

annual_juvenile_mortality_dumps = RANDOM(min_juv_mort_rate_dumps, max_juv_mort_rate_dumps)

annual_juvenile_mortality_rate = RANDOM(min_juv_mort_rate, max_juv_mort_rate)

chick_mortality_rate = RANDOM(min_chick_mort_rate,max_chick_mort_rate)

chick_mortality_rate_dumps = RANDOM(min_chick_mort_rate_dumps,max_chick_mort_rate_dumps)

clutch_size = RANDOM(min_clutch_size,max_clutch_size)

clutch_size_dumps = RANDOM(min_clutch_size_dumps, max_clutch_size_dumps)

egg_unviability_rate = RANDOM(min_egg_unv_rate,max_egg_unv_rate)

egg_unviability_rate_dumps = RANDOM(min_egg_unv_rate_dumps,max_egg_unv_rate_dumps)

OTHER VARIABLES

seasonality = COUNTER(0,12)

SWITCHERS

culling_option = 0/1

dump_option = 0/1

egg_destruction_option = 0/1

CONSTANTS

max_adult_mort_rate = 0.23

max_adult_mort_rate_dumps = 0.11

max_chick_mort_rate = 0.866

max_chick_mort_rate_dumps = 0.548

max_clutch_size = 2.66

max_clutch_size_dumps = 2.90

max_egg_unv_rate = 0.439

max_egg_unv_rate_dumps = 0.292

max_juv_mort_rate = 0.72

max_juv_mort_rate_dumps = 0.33

min_adult_mort_rate = 0.16

min_adult_mort_rate_dumps = 0.077

min_chick_mort_rate = 0.778

min_chick_mort_rate_dumps = 0.526

min_clutch_size = 2.37

min_clutch_size_dumps = 2.63

min_egg_unv_rate = 0.372

min_egg_unv_rate_dumps = 0.172

min_juv_mort_rate = 0.47

min_juv_mort_rate_dumps = 0.17
culling_intensity = 0.62
culling_timing_finish = 228
culling_timing_start = 193
laying_season_final_month = 4
laying_season_inicial_month = 3
dump_timing_finish = 288
dump_timing_start = 0
egg_destruction_finish = 468
egg_destruction_intensity = 0.42
egg_destruction_start = 253
nesting_area_m2 = 3.8
total_area_berlenga_m2 = 990000

Appendix O - Variation in the yellow-legged gull demographic parameters (+/- 10% and +/− 50%), using the original input space of all parameters fixed to their mean value (original value).

Parameter	Original value	Minus 10%	Plus 10%	Minus 50%	Plus 50%
Adult mortality rate	0.20	0.18	0.21	0.10	0.29
Adult mortality rate dumps	0.09	0.08	0.10	0.05	0.14
Juvenile mortality rate	0.60	0.54	0.65	0.30	0.89
Juvenile mortality rate dumps	0.25	0.23	0.28	0.13	0.38
Clutch size	2.52	2.26	2.77	1.26	3.77
Clutch size dumps	2.77	2.49	3.04	1.38	4.15
Egg unviability rate	0.41	0.36	0.45	0.20	0.61
Egg unviability rate dumps	0.23	0.21	0.26	0.12	0.35
Chick mortality rate	0.82	0.74	0.90	0.41	1.00*
Chick mortality rate dumps	0.54	0.48	0.59	0.27	0.81
Egg destruction effort	0.43	0.39	0.47	0.22	0.65
Culling intensity	0.62	0.56	0.68	0.31	0.93

*Parameters truncated to 1, since with the implemented variation the parameter attained values greater than 1

Appendix P - Sensitivity analysis (one-parameter-at-a-time) carried out for the yellow-legged gull breeding population size, given +/− 10% and +/−50% variation in demographic parameters, for each scenario considered. The result measures the percentage of change in the abundance of breeding birds between simulations with and without variation in the demographic parameter under study, for June 2016 (t=462) in the retrospective scenarios (Baseline, scenario 1, 2 and 3) and June 2040 (t=750) in the prospective scenarios (scenario 4 and 5).

Parameter variation	Annual adult mortality rate	Annual adult mortality rate dumps	Annual juvenile mortality rate	Annual juvenile mortality rate dumps	Clutch size	Clutch size dumps	Egg unviability rate	Egg unviability rate dumps	Chick mortality	Chick mortality dumps	Culling intensity	Egg destruction effort
Baseline scenario												
-50%	219,95	143,83	16,44	29,29	-39,43	-87,57	32,86	61,22	56,65	161,61	132,13	51,50
-10%	25,32	19,19	2,79	5,04	-8,70	-29,24	6,17	10,47	8,84	20,96	12,20	9,24
+10%	-19,95	-15,98	-2,59	-4,71	9,12	37,94	-5,98	-9,68	-7,89	-17,25	-6,37	-8,73
+50%	-66,11	-57,59	-11,35	-20,69	49,90	315,35	-27,99	-41,33	-16,04	-60,93	-28,25	-38,90
Scenario 1												
-50%	210,34	143,14	21,88	29,73	-72,31	-92,68	44,28	62,59	77,59	166,01	129,25	0,00
-10%	24,58	19,12	3,66	5,12	-11,31	-29,70	8,15	10,67	11,69	21,37	9,89	0,00
+10%	-19,47	-15,93	-3,38	-4,77	12,06	38,74	-7,80	-9,84	-10,27	-17,54	-8,29	0,00
+50%	-65,11	-57,48	-14,70	-20,95	68,05	119,59	-35,62	-41,91	-20,70	-61,62	-29,72	0,00
Scenario 2												
-50%	0,00	330,47	0,00	43,45	0,00	-94,25	0,00	94,02	0,00	280,90	126,84	66,05
-10%	0,00	33,30	0,00	7,15	0,00	-38,02	0,00	14,79	0,00	30,18	9,88	9,22
+10%	0,00	-24,82	0,00	-6,54	0,00	56,22	0,00	-13,14	0,00	-23,05	-8,29	-13,75
+50%	0,00	-75,46	0,00	-27,73	0,00	626,93	0,00	-52,13	0,00	-72,62	-29,72	-50,01

Scenario 3												
-50%	0,00	322,80	0,00	46,98	0,00	-95,43	0,00	102,82	0,00	315,35	126,84	0,00
-10%	0,00	32,83	0,00	7,65	0,00	-40,09	0,00	15,88	0,00	32,54	9,89	0,00
+10%	0,00	-24,55	0,00	-6,97	0,00	61,01	0,00	-13,99	0,00	-24,46	-8,29	0,00
+50%	0,00	-75,04	0,00	-29,34	0,00	723,36	0,00	-54,60	0,00	-75,12	-29,72	0,00
Scenario 4												
-50%	2050,12	143,79	57,59	29,26	-79,37	-87,59	141,12	61,19	300,14	161,56	127,27	191,46
-10%	81,36	19,15	8,54	5,03	-24,73	-29,26	20,49	10,43	30,13	20,95	9,88	25,61
+10%	-44,39	-16,01	-7,57	-4,71	31,15	37,93	-17,49	-9,69	-22,61	-17,26	-8,31	-21,04
+50%	-94,23	-57,59	-30,27	-20,72	249,56	315,27	-64,28	-41,35	-42,09	-60,91	-29,72	-72,08
Scenario 5												
-50%	1949,71	143,83	69,19	29,28	-84,74	-87,57	175,96	61,22	390,81	161,61	127,30	75,17
-10%	79,68	19,18	10,02	5,04	-28,25	-29,25	24,19	10,47	35,78	20,95	9,89	12,67
+10%	-43,86	-15,97	-8,73	-4,70	37,03	37,94	-20,11	-9,68	-25,89	-17,26	-8,30	-11,61
+50%	-93,97	-57,58	-34,35	-20,70	321,09	315,35	-70,36	-41,32	-47,32	-60,91	-29,73	-72,08