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Coordination in parental foraging and chick provisioning on temperate and tropical environments

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2022

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temperate and tropical environment

2023

Mestrado em Biologia Marinha

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UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia 2022

UNIVERSIDADE DE COIMBRA

Faculdade de Ciências e Tecnologia
2022

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II.

a. **Abstract**

Parental care is, for most mammal species, a behaviour only present in the female. Studies showed that 95% of mammal species exhibit female-only care, and the remaining 5% of species will show biparental care. In birds, however, the vast majority of species will show biparental care, both during incubation and while rearing the growing chicks. To incubate the egg and feed the growing chick periodically, is very energy-consuming for the parents, which is why, while breeding, bird parents need to display a certain degree of synchrony in their behaviour. This is especially relevant for pelagic seabirds, often engaging on long and distant forays. Animals will allocate a large proportion of their time and energy in foraging, and this foraging is limited by the mobility, distribution, abundance and predictability of food resources. On top of that, conditions at sea are much more challenging and variable than inland conditions. At sea, food resources can change drastically, not only in sheer amounts, but also in location. Individuals must therefore be able to identify, understand and adapt to marine environmental drivers around them and their breeding location, in order to successfully locate prey for themselves and their nestlings. The long distances, as well as the long periods that foraging trips can take for each parent, will further challenge the coordination between mates, at-sea or at-colony, to successfully and efficiently provide for their growing chick at the nest. Such behavioural adaptation has been studied in seabird species inhabiting temperate marine regions, where the resource availability is comparatively more predictable. But those adaptations are much less studied in more variable environments, such as a tropical marine biota. Tropical marine habitats are characterised by broadly oligotrophic water regimes, with likely low prey availability and abundance and seabirds need to adapt to a likely patchier distribution of their prey for thriving in this environment. In order to better understand the extent of tropical species' behavioural adaptation capabilities, we decided to investigate the inter-sexual coordination in foraging behaviour and chick provisioning of the Cape Verde Shearwater *Calonectris edwardsii*, and compare them to the Cory's Shearwater *Calonectris borealis*, a species thriving in more temperate regions than the tropical waters of Cabo Verde. To do so, we deployed GPS-loggers on parents during mid chick-rearing period, to track their foraging movements, and understand how environmental proxies of productivity drive their foraging decisions and how those foraging choices reflect on their body condition and that of their growing.

Our study showed a clear difference between both species. While *Calonectris edwardsii* reacts and adapts very strongly to its environment, and any changes in it, *Calonectris borealis* seems to rely more on the constant food resources, typical of the temperate and productive environment it lives in. However, both species showed a good learning capacity and potential of behavioural adaptation. Even though they live on very different environment, and thus behave quite differently, both populations show that they are capable of adaptations, which suggest they would keep a good fitness, even through the up-coming modifications due to climate change and anthropic activities

Keywords: Adaptation, Procellariforms, foraging behaviour, environment drivers, chick growth

b. Resumo

Nos ultimos anos, perceber e controlar as alterações globais devido a actividades humanas tornou-se uma prioridade não só para a pesquisa cientifica, mas tambem para a responsibilidade civil. Com as recentes mudanças no clima, e todas as concequencias para o meio ambiente, em tempos em que tentamos entender como nos adaptar, como sociedade, para superar essas situações terríveis, os cientistas têm se perguntado mais do que nunca como poderiam a fauna e a flora sujeitas a essas mudanças adaptar-se e viver através delas.

A Terra passou por varias fases de evolução, e a fauna sempre se adaptou ao seu ambiente, em diferentes escalas. Mas, recentemente, as actividades do ser humano trouxeram mudanças ambientais de uma magnitude sem precedentes. Os cientistas estão documentando cada vez mais acerca dos impactos das atividades antrópicas sobre os animais selvagens, e principalmente nas mudanças de comportamento. Isso é explicado pelo o fato que para muitas espécies, a primeira resposta a essas mudanças serão os ajustes comportamentais, que podem levar ao surgimento ou à perda de tradições em certas espécies usando o aprendizado social como transmissão de comportamentos (Gruber et al., 2019). Tais respostas podem dar tempo para que as mudanças genéticas surjam, facilitando assim as adaptações de longo prazo às novas condições ambientais (Tuomainen & Candolin, 2011). No entanto, eles também alertam que tais respostas comportamentais também podem levar a uma diminuição na aptidão populacional, pois essas mudanças se concentrarão no bem-estar do indivíduo e não da população. Embora sejam importantes para a sobrevivência imediata, as respostas

comportamentais nem sempre são adaptativas, nem a plasticidade comportamental é sempre suficiente para contrariar a magnitude de algumas mudanças ambientais (Wong & Candolin, 2015). Um dos grupos de animais mais estudado nessa matéria são as aves.

Por serem extremamente diversificadas, amplamente distribuídas e apresentarem uma complexidade comportamental e de organização social semelhante à dos mamíferos, e ainda serem facilmente acessíveis em ambientes naturais, as aves sempre foram excelentes objetos de estudos em biologia e uma pedra angular na evolução da etologia (Konishi et al. , 1989; Turner, 2007). As aves marinhas, em particular, são bioindicadores extremamente bons de seu ambiente, muitas vezes sendo predadores de topo e omnipresentes (Burger & Gochfeld, 2004). Devido ao ambiente hostil em que vivem, as aves marinhas geralmente formam laços de pares de longo prazo (Black & Hulme, 1996). Como a disponibilidade de recursos alimentares no seu território pode variar, os pais devem organizar o seu investimento entre o cuidado da cria e sua automanutenção. Esse equilíbrio é importante ser realisado para não comprometer o sucesso reprodutivo futuro dos pais (Gillies et al., 2021; Stearns & Stephen C., 1992; Trivers , 1972). Os casais reprodutores só podem beneficiar em coordenar as suas atividades de cuidado ((incubação do ovo, viagem de forrageamento do filhote, proteção do ninho etc.) Gillies et al., 2021). Essa necessidade da coordenação vai ser particularmente importante para as aves marinhas. Como os pais se alimentam geralemente em zonas mais distantes do que os arredores imediatos das colonias, a competição entre o abastecimento de comida para a cria e o autocuidade necessário aos adultos vai ser muito mais rígida.

Para resolver este problema, muitos procellariiformes apresentarão um comportamento de Dual Foraging (Paiva et al., 2010; Tyson et al., 2017). Os pais alternarão então as viagens de forrageamento longas (LT) e curtas (ST), de acordo com sua própria necessidade. A viagem longa servirá para a automanutenção do adulto, enquanto a viagem curta servirá apenas para o aprovisionamento da cria. Vários estudos (John Warham, 1990; Swatschek, 1994) provaram a existência deste comportamento tanto em *Calonectris borealis* como em *Calonectris edwardsii*, as especies que escolhemos para realisar o nosso estudo. Estudos recentes sugerem que o desenvolvimento e crescimento da cria, e também, o sucesso reprodutivo do casal, pode estar diretamente relacionado à forma como foi realizada a coordenação da viagem entre os pais (Wojczulanis-Jakubas et al., 2018).

Os benefícios da coordenação de pares já foram discutidos e comprovados para muitas espécies (Tyson et al., 2017; Wojczulanis-Jakubas et al., 2018), mas ainda falta o entendimento sobre o que exatamente a desencadeia. Estudos sugerem que uma interação física entre os pais é necessária para manter a coordenação no seu máximo potencial (Gillies et al., 2021), ou que os pais baseiam os seus esforços no comportamento de mendicância da cria (Gillies et al., 2021). Isso mostraria um certo nível de plasticidade do comportamento de forrageamento (Cerveira et al., 2020), para cada indivíduo, a fim de adaptar seu comportamento a pistas externas. Grissot et al. (2019) também mostraram que os fatores ambientais têm impacto no comportamento de forrageamento de certas espécies.

Infelizmente, ainda faltam dados sobre o assunto. Grissot et al. (2019) concluem o seu estudo afirmando que, embora seja altamente provável que os fatores ambientais afetem o comportamento de forrageamento dos casais reprodutores, ainda é incerto em que grau e em que medida a coordenação é uma resposta plástica dos pais para o ambiente de forrageamento. Eles afirmam que "o alcance da variação ambiental ainda pode estar abaixo de um limiar crítico de condições extremas que desencadeariam modificações mais pronunciadas nos padrões e coordenação de forrageamento dos pais". A maioria dos estudos sobre o assunto tem sido feito em ambiente temperado ou ártico, e apenas estudos recentes abordam esse problema em ambiente tropical (Cerveira et al., 2020), tentando preencher a lacuna de conhecimento em torno dessas áreas.

No nosso estudo, pretendemos (1) entender como vários fatores ambientais (Bathymetry BAT, Ocean Mixed Layer Depth OML, Sea Surface Temperature SST, Net Primary Production NPP, e Nekton concentration in the Epipelagic Layer EPI) impactam de forma diferente os indivíduos e a coordenação dos pares, (2) o quanto um casal reprodutor pode adaptar seu comportamento às mudanças no seu ambiente, (3) comparar como uma população de região temperada e uma de uma região tropical reagirão a mudanças nos mesmos fatores ambientais. Finalmente, esperamos ver se existe uma correlação entre as mudanças no comportamento de forrageamento dos pais e o crescimento de seus filhotes, para entender como as mudanças em determinados fatores ambientais podem afetar a aptidão das populações. Até onde sabemos, este estudo é a primeira compilação de tantos fatores, bem como a comparação entre diferentes populações, em diferentes ambientes. Deve ajudar a entender melhor e computar como as populações de aves marinhas podem evoluir nos próximos anos, como resultado das alterações climáticas que impactam nas suas áreas de

vida.

O nosso estudo mostra uma real differencia entre as duas especies. Enquanto *Calonectris edwardsii* vai reagir de forma muito prononciada as modificações no seu ambiante, *Calonectris borealis* parece confiar mais nas reservas alimentares constantes do seu meio ambiante. Embora essas differencias comportamentais, as duas species mostraram capacidade de aprender e adaptar-se as modificações dos seus meios ambiantes.

Palavras chaves: Adaptação, procelariformes, comportamento de busca alimentar, cambios ambientais, crescimento da cria

III. Acknowledgements

This work could never have been achieved alone, and so I wish to thank several people that helped me along the way.

I thank Vitor Paiva and Ester Serrão for being my supervisors and helping me on all aspects of this project.

I thank BIOSFERA for the amazing work they are doing in Cabo Verde, doing everything they can to protect and preserve Nature, allowing scientist and researcher to get incredible data from this wonderful ecosystem.

I thank the ICNF guards working in the Berlengas natural reserve for their work and for allowing me to learn from them while on the island.

I thank Bennedikt Brunner for the understanding and the time he gave me to work on this thesis while helping him on his project, as well as for the truly helpful statistic classes he offered us.

Finally I wish to thank the head professor of the Marine Biology Master of Faro, Rita Castilho for all the time and support she has given me, and all the work she has done on this master program.

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List of abbreviation:

- EPP: Environmental Polygamy Potential
- ST: Short Trips
- LT: Long Trips
- BAT: Bathymetry
- OML: Ocean Mixed Layer
- SST: Sea Surface Temperature
- NPP: Net Primary Production
- EPI: Nekton concentration in the Epipelagic Layer

General Introduction

Animal behaviour has always fascinated mankind. Darwin stated that each species had its own set of behaviours, just like they have their own anatomical properties (Darwin 1850). Ethology, the study of animal behaviour, has since then tried to discover and understand the complexity of all the different behaviours observable. Mating behaviour has always been a prime subject of ethology, each species, and almost every individual having their own distinct way of expressing them, and has always been a much-studied subject. Reproductive behaviours are a fundamental point of the theory of evolution by natural selection, as Darwin pointed out, it is one of the principal causes of said evolution.

IV. Environmental drivers

Environmental changes have been defined as a change or disturbance of the environment caused by natural ecological processes and human influences (Johnson et al., 1997). It includes various factors, such as natural disasters, human interferences or animal interaction. Environmental changes may encompass not only physical changes but also factors like an infestation of invasive species

Changes in temperature, light or even pH will greatly impact a number of species depending on those variables. "Temperature is the most important single factor governing the occurrence and behaviour of life" (Gunter, 1957), and later studies showed that this variable, on top of modifying the direct environment of the individuals, could also affect their physiological performance (Kinne, 1970).

Changing global temperatures, which modify weather patterns, will cause a change of the timing of resources (Bradley et al., 1999; Dunne et al., 2003; Edwards & Richardson, 2004; Thackeray, 2010). Thus, species relying on seasonal resource availability for reproduction will need to adjust the timing of reproduction and other life events (i.e. migration) to be able to cope with spatio-temporal shifts of their usual resources (Both et al., 2009; Travis et al., 2013)

For marine predators, such as seabirds, climate induced variability of prey availability, and its subsequent distribution, is a dominant factor for the regulation of their lifetime reproductive fitness and population viability. We know that large-scale atmospheric climate circulation and ocean productivity are closely related, the first impacting severely on the second one. These then have the potential to affect seabirds at both local and basin scales (Barbraud & Weimerskirch, 2003; Barrett et al., 2013; Sandvik & Einar Erikstad, 2008)

In order to survive such changes, the fauna has gone through an extensive number of adaptations, and still does. From morphological change to an all-new behaviour, wildlife never stops evolving in order to cope with their ever-changing environment.

V. Adaptations

a. Physical

The easiest adaptation to observe are of course the morphological, and physical evolutions. In order to adapt to any environment, organisms have taken all sorts of shapes and sizes. In 1847, Carl Bergmann published some observations on the body size of mammals (Bergmann, 1847). He stated that the endothermic body size increased with increasing latitude. Bergmann's rule states that selection will favour, within species, individuals with larger body sizes in cooler temperatures, because the total heat loss would be diminished through lower surface area to volume ratio. In other words, individuals living in colder regions will present a bigger body mass. Even though this "rule" is quite vague and contested, studies found that over 72% of birds and 65% of mammal species follow it, and the overall tendency to follow the rule occurs also within orders and families (Meiri & Dayan, 2003). Darwin's Theory of Evolution itself is based on the observation of morphological adaptation, of several species of finches. Darwin observed that different species of finches evolved to have very different beak size and shapes, each specialised for the diet of the species

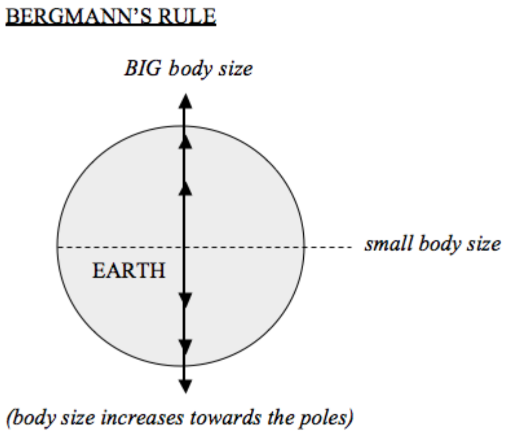


Figure V-1: Schematic showing a simplified Bergmann's rule (https://controverses.sciences-po.fr/climateblogs/shrinkingsheep/subcontroversies/bergmanns-rule/index.html)

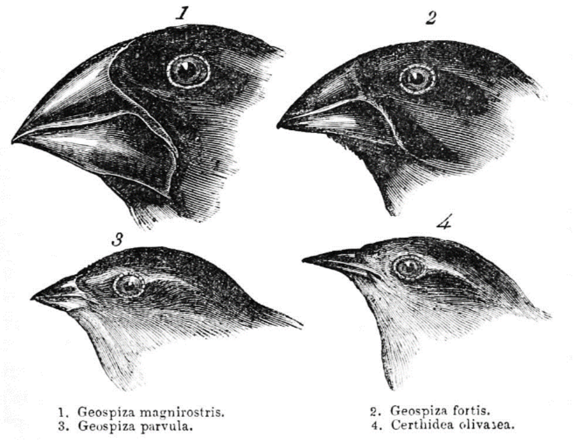


Figure V-2: Drawing representing four species of Finches of the Galapagos, described by Darwin. (John Gould (1804-1881), from "Voyage of the Beagle")

But morphological modifications are not enough adaptations to survive. Many species will also, and primarily modify their behaviour to better cope with their environment.

b. Behavioural

Some adaptive behaviours are quite easily observed and thus studied. Migration is a perfect example of behavioural adaptation. In 2019, the National Geographic Society defined, in its Encyclopaedia, migration as "a pattern of behaviours in which animals travel from one habitat to another in search of food, better conditions or reproductive needs."

Studies also suggest how ancient Micronesians and Polynesians used bird migration in their traditional land finding techniques, more than 3000 years ago (Lewis, 1972). But a number of different organisms will migrate, showing that this evolution happens because of the environment and not the genes of the organisms. It has since been accepted that some species, namely long-lived ones, will learn those behaviours through their life (Campioni et al., 2020). It is now a proven fact that learning, as well as other adaptive changes in their behaviour, based on past experience (Dukas, 2004; Shettleworth, 1999), will have a serious impact on every aspect of animal behaviour, and potential fitness implications (C. R. Brown et al., 2008; Raine & Chittka, 2008).

Other adaptations also appear in order for the organism to adapt to a harsh environment, like the fact that some organisms will create food reserves to last through winter, while others will simply hibernate.

But one particular set of behaviours is not directly linked to the environment, but more to the relationship between individuals of the same species: the mating behaviours.

VI. Evolution of mating behaviours

a. Main reproductive systems

i. Polygamy

In sexual reproduction, several types of mating behaviours can be observed. Each of them have their own evolutionary history, being adaptations form several different external factors. One of, if not the most, spread behaviour is Polygamy. The environment may have some drivers, that would influence the appearance polygamy in the species evolving in it, “Environmental Polygamy Potential” (EPP) (Emlen Stephen T. & Oring, 1977). EPP increases, positively correlated to the spatial increase of resources in the territory, and lack of synchrony in the availability of patterns. Lack of homogeneity and superabundant food resources in the environment will also affects further evolution of polygamy (Csermely & Cserhlely, 1984). In species using a sexual reproduction, it is often observed that one sex initially presents more parental investment. It is mostly female, since producing gametes of larger size and lesser amount. This lead directly, via sexual evolution, to Polygamous reproduction systems (Csermely & Cserhlely, 1984). The changes in environment would then lead to the evolution of this behaviour, giving rise to loads of different adaptative sexual evolution. Monogamy seems to be one of those adaptatin, apearing later in evolution, as the sexual adaptation to harsh conditions and habitats (Wickler & Seibt, 1983; E. O. Wilson, 1975).

ii. Monogamy

This behaviour would be clearly advantageous for species living in rather harsh and poor environments, with very few trophic resources (Csermely & Cserhlely, 1984). What’s more, if a pair stays together from one season to the next, the usual intraspecific competition would be reduced. Thus, the reproductive period will be put forward, since long periods of time, usually used for courtship and partner choice, would not be necessary.

iii. Birds mating system

Our work's subjects are bird species. For this group, we can see both polygamy and monogamy, sometimes even present in the same species. The change from one behaviour to another will depend on the resources available in the environment. A study on the mating habits of wrens (*Troglodytes troglodytes*) discovered that colonies on small island, off the coast, and thus with lower food availability, would present monogamous couples, while the wrens' colonies on the continent, having larger foraging habitats were polygamous (Armstrong, 1955). For birds of Paradise, the diet itself could influence whether the bird would go towards a polygamous or monogamous mating system (Beehler, 1983).

However, fidelity (Monogamy) seems to prevail and appears to be the rule for most species of birds. In birds, the evolutionary drive towards either monogamy or polygamy would be the result of the interaction between food availability in the environment and Parental investment (Graul, 1977).

b. Parental investment

In Metazoa animals, intraspecific sexual selection and dimorphism are linked to the differentitaion between the parental roles for both sexes. Together with anisogamy, this will lead to the differing amount of involvement of an individual towards its offspring. A study trying to search for a genetic-evolutionary reason to explain that, elaborated the theory of *Parental investment* (Trivers, 1972). "Investment is defined as the cost of any act performed by an adult to the benefit of its offspring enhancing the survival chance of its offspring, i.e. its genetic fitness, and at the same time limiting the parent's capacity to invest in other offspring" says Csermely, explaining Trivers' theory (Csermely & Cserhlely, 1984). Parental care represents a direct defence of personal productive investment. For Trivers, investment can be translated to energy expenses. Due to anisogamy, females will invest more during fertilisation, as an egg is more expensive than a spermatozoon. More researchers agreed with this theory, and some studies stated that the parent investing most will prefer to stay with the offspring and care for it, while the other one, having invested less, might be tempted to desert it (Dawkins & Tamsie, 1976) . While this statement has been proved for many species, research has shown many other species with completely different Investment Dynamics.

i. Two main strategies

The life history strategies of animals can be broadly categorised using their reproduction rate and longevity. This creates a continuum where animals will adopt two possible strategies, r or K. For both of them, the amount of parental care needed for the offspring is a decisive factor

1. R strategy

R selected organisms are short-lived, producing numerous offspring which will develop quickly, and require low to no parental investment (Promislow & Harvey, 1990). This strategy will allow r-selected populations to grow exponentially in environments with high seasonal temporality. It also allows them to quickly establish new territories in adjoining and disturbed environments (J. B. Williams et al., 2010) This strategy is then characteristic of an unstable and harsh environment. And with restricted generational rhythms, this strategy will allow the population to fluctuate according to the environmental conditions

2. K strategy

On the other hand, K strategy applies to larger and long-lived species. They will produce a small number of offspring but will present a great parental investment. We will also observe an important intraspecific competition for the resources. Those organisms will prosper in stable habitats (at least over the long-term), which will favour their long lifetime, allowing the population to persist near, or at, carrying capacity (Odum & Barrett, 2005; C. K. Williams, 2013)**.** Long lived species will prioritise investment in growth and maintenance, since there is a high competition for ressource between conspecifics. Therefore, when resources are scarce, many will opt not to reproduce, enhancing the adult's survival chances, and the future reproductive fitness (Bool, 2018).

Figure VI-1: "Example of r and K marine species. r-selected species on the left, k-selected on the right, above the line. Scale is non-linear and life expectancy (years) as well as the number of offspring shown below the line are approximate are presented for illustration purposes only" Bool, 2018.

In general, Invertebrate and Ectotherm vertebrates will tend towards the r strategy, while Mammals and Birds will tend toward K selection. Nonetheless we can observe both models among the same Phylum or Class. As an example, studies showed that bird species with precocious offspring will tend towards the r model, while those with altricial offspring will appear to follow the K (Gubernick, 1981).

With the actual climate change progressing at an alarming speed, many species, mostly following the K-strategy, will suffer due to their lack of adaptability. As a simple example, studies showed a clear decrease in the population of major tits (*Parus major*), particularly the mass and numbers of fledglings. This decrease was correlated to an increasing mismatch in the timing of food resources (i.e. peak caterpillar biomass) and when the birds began breeding (Visser et al., 2006) . Considerable evidence show that many taxa will not be able to adapt fast enough, due to their reliance on seasonal food peaks, and the fact that they have restricted periods of time for producing offspring ((Bool, 2018; Bronson, 2009; Burthe et al., 2012; Nussey, 2005; Thackeray, 2010)

ii. Who will perform the parental care and investment?

In the vast majority of species, with both precocious and altricial offspring, parental duties are performed by one of the parents. In Arthropods and Ectothermic Vertebrates, the male will more often perform those duties, while in Homeotherms, females are usually the ones looking after the young ((J. L. Brown, 1975)). Studies show that 95% of mammal species exhibit female-only care, and the remaining 5% of species will show biparental care.

But for birds, most species will show biparental care, both during incubation and while rearing the growing chicks. Tending to the eggs, then to the nestling, is very energy consuming for the parents, which is why, while breeding, bird parents need to display a certain degree of synchrony in their behaviour. This is especially relevant for pelagic seabirds, often engaging on long and distant forays. Animals will allocate a large proportion of time and energy to foraging, and this foraging is limited by the mobility, distribution, abundance and predictability of the food resources. On top of that, conditions at sea are much more challenging and variable than in-land conditions. In order to keep their reproductive fitness, pelagic birds' parents will have evolved in ways to counter this tough environment, and developed behaviours enabling them to provide for their nestling needs.

Parental care in birds can be done by one of the parents, but only in species with precocious offspring, when the resources of the environment are so abundant, that the parent can easily forage enough to sustain the nestlings and itself (Morse, 1963).

Parental care is especially linked to Monogamy. Since this latter has probably evolved from Polygamy, as an adaptation to a harsh and poor environment (Csermely & Cserhlely, 1984), the logical "follow up" adaptation to low resources was close cooperation between partners.

VII. Seabirds

a. Ecology

i. Seabird life history adaptation in a changing climate

Sea-birds, as a general group, will present a vast array of physiological and life-history traits, which evolved to adapt in the marine environment, an environment known for the important temporal variability and patchy distribution of food items. (Weimerskirch, 2007).

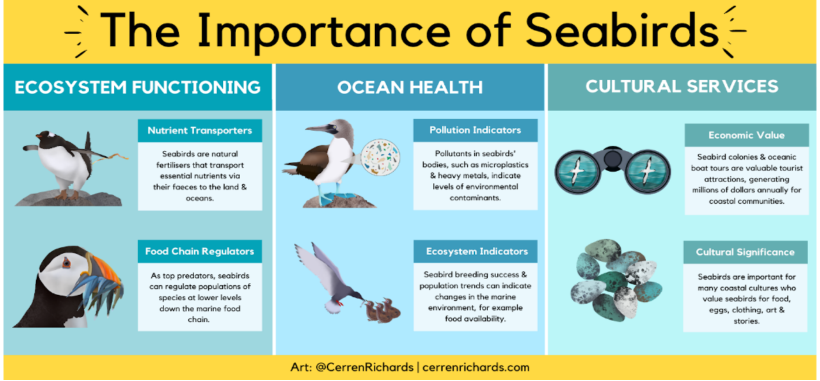
To survive in this harsh competitive environment, and be able to procure these patchily distributed resources, this group evolved, presenting both morphological and behavioural adaptations (Catry et al., 2013; Ricklefs, 1990; Stearns, 1977).

Such adaptations can be observed in the flightless penguins, and reduced flight performances of auks, whose wings have taken a fin-like shape in order to favour diving and swimming performances (Elliot et al., 2013). Procellariiformes birds present a number of physical adaptations allowing them to minimise the cost of flying, and thus, they can expand their foraging areas, searching for prey over great distances (Warham, 1977; Weimerskirch et al., 2000). Many species present long migrations (Alerstam et al., 2003; Fort et al., 2013), while others have adaptations specialised in prey capture, e.g., dive behaviour (Kato et al., 2006) and some have very specific diets (Croxall & Prince, 1980)

As an example, studies on the Giant petrels (Macronectes spp) and kelp gulls (*Larus dominicanus*), respectively, showed that those species obtained from scavenging on carrions, as well as obtaining prey directly in the sea (Favero & Silva, 1998; Gonzalez-Solis et al., 2000). This kind of diet was categorised as Type A Generalists, and Type B Generalists as populations with a narrow dietary niche (Bearhop et al., 2004). For *Una lomiva*, even though the population as a whole is considered generalist, consuming a wide array of prey, the individuals themselves can be specialised in one type of prey (Hamish et al., 2009). For some species, we can observe a sex-related diet specialisation, mostly during chick rearing period, even though in no species was observed a trophic difference between sexes (Phillips et al., 2011). Several studies stated that in a population, the fact of partitioning resources between conspecifics will increase the individual foraging success, because it reduces the intra-specific competition (Bolnick et al. 2003; Ceia & Ramos, 2015). Such behaviour would buffer the population against the decline of any single food type. Specialist bird populations, populations having a narrower dietary niche, will have a harder time coping with a rapidly changing climate, thus changing the food resource repartition or mass, than the generalists' populations (Forcada & Trathan, 2009; Grémillet & Boulinier, 2009; Jenouvrier et al., 2014; Joiris, 2017). It has been shown that both spatial and temporal foraging strategies exhibited by seabirds are dependent on extrinsic factors, such as prey distribution and availability. Which can themselves be driven by oceanic conditions, and intrinsic factors, as individual specialisation, stage of breeding, age, sex, morphology and season (Cerveira et al., 2020a; van Donk et al., 2019; Votier et al., 2017). Birds are capable of memorising different foraging areas as well as the successfulness of the foraging attempt, to later go back to them (Fernández et al., 2001). So, it's expected to find a higher proportion of seabirds in the highly productive foraging sites and the predictable foraging sites (Hamer et al., 2001; Irons, 1998; Weimerskirch, 2007). However, studies on tropical areas did not show such consistent patterns in the foraging site fidelity of birds (Cerveira et al., 2020). It has been shown that the main reason for such a difference on foraging patterns is that seabirds appear to heavily rely on underwater predators, driving prey to the surface, for their own foraging (Au & Pitman, 1986). And such events are much less predictable than the static oceanographic variables that birds in more moderate environments.

ii. The importance of seabird populations

Seabirds are predators, highly placed in the marine food webs, and as such, have a high potential as monitors for pollutants accumulated at trophic levels, but also monitors of fish stocks (Furness & Camphuysen Furness, 1997). And besides being a very heterogenous group, presenting a number of physiological and behavioural differences among species, they broadly share several life-history strategies, following the K strategy, as long-lived, with low reproductive rates, slow chick development and delayed sexual maturity (Bool, 2018; Ricklefs, 1990). Measure a number of *vital* rates such as annual variability of breeding effort, diet and foraging distribution or reproductive success (Cubaynes et al., 2011; Frederiksen et al., 2012; Horswill et al., 2017). A faster way to understand how climate change impacts seabird populations than through the monitoring of population size trends, would be to measure the breeding chronology and the chick conditions, as variability in those intrinsic rates will provide an indication of how the climate influences the population (Chambers et al., 2015). And, due to their reproductive strategy (K), adults will be more likely to ensure their survival rather than that of the chick, if need be, so studying breeding success will show an among year variability, more readily than only adult survival would (Barbraud et al., 2011) Climate change is bound to also disturb the food distribution in the oceans. This will surely disrupt the foraging habits of the seabird population. Understanding the foraging ecology (where and how seabirds find food resources) will then provide a greater insight on the influence that climate change has on them (Morales et al., 2010).


The Importance of Seabirds

ECOSYSTEM FUNCTIONING

Nutrient Transporters

Seabirds are natural fertilisers that transport essential nutrients via their faeces to the land & oceans.

Food Chain Regulators

As top predators, seabirds can regulate populations of species at lower levels down the marine food chain.

OCEAN HEALTH

Pollution Indicators

Pollutants in seabirds' bodies, such as microplastics & heavy metals, indicate levels of environmental contaminants.

Ecosystem Indicators

Seabird breeding success & population trends can indicate changes in the marine environment, for example food availability.

CULTURAL SERVICES

Economic Value

Seabird colonies & oceanic boat tours are valuable tourist attractions, generating millions of dollars annually for coastal communities.

Cultural Significance

Seabirds are important for many coastal cultures who value seabirds for food, eggs, clothing, art & stories.

Art: @CerrenRichards | cerrenrichards.com

Figure VII-1: Schematic representing the different roles of seabirds (Cerren Richards, Twitter)

iii. Foraging behaviour

1. Foraging ecology

Seabirds are central-place foragers, meaning their breeding success depends on the presence of food resources within foraging distance of their land-based nests. Seabirds must balance the distance they travel to, to provision themselves and the chick (Orians & Pearson, 1979). During breeding season, nutrient poor waters around the colony and intra- or interspecific competition might decrease the reproduction fitness of the couples, reducing the amount of food resources available for their and the nestling. This contributed to the evolution of a bi-modal foraging habit (*see b. Special Mating habits)*, during breeding season, very common among Diomedeidae and Procellariidae (Baduini & Hyrenbach, 2003; Congdon et al., 2005; Welcker et al., 2009, 2012).

Seabirds do not return to land-based nests outside of the breeding period. During the rest of the year, they will spend all of their time at sea. Even Though, they still need to recover the energy lost during the breeding period, and create new energy reserves, for the future reproductive effort (Daunt et al., 2006; Sorensen et al., 2009). They are then extremely sensible to fluctuations in food availability. In the case of nonlinear climate events, the prey availability can be reduced, thus reducing the bird's capacity to start the breeding activities, in time or at all, and in the worst-case scenario, also lower the adult's survival (Baduini et al., 2001; Barbraud & Weimerskirch, 2003). Several studies showed, all year round, seabird foraging behaviour was heavily impacted by ocean productivity (Chlorophyll *a* concentration) and environmental variability, e.g., changing SST (Sea Surface Temperature), wind strength, water thermal structure etc. (Carroll et al., 2016; Einoder et al., 2013; Kokubun et al., 2010; Weimerskirch et al., 2012; R. P. Wilson et al., 2002). Thus, we can expect that strengthening our understanding of the foraging habits of seabirds, both during and outside breeding season, will help us understand how those populations respond to climate variability.

2. Monitoring the foraging behaviour

A number of tracking devices now exists, helping seabirds' ecologists to study where animals find their prey (R. P. Wilson & Vandenabeele, 2012). Studies have come to a listing of some devices easily attachable to the animal, thus giving precise information on its movement (L. J. Wilson et al., 2009). It is the case for VHF (Very High Frequency) telemetry, PTT (Platform Terminal Transmitters) as well as GPS (Global Position System) and GLS (Global

Location Sensors). They will all provide varying levels of information on foraging metrics. For example:

- GLS loggers record light levels. This data is used to estimate day length, using the sunrise and sunset twilight occurrence time. This will permit to coarsely calculate longitude and latitude of the logger, and thus of the animal, at those times. Note that some GLS are even capable of recording SST which, once cross-referenced with light data, can provide a more accurate location estimate. They will also record dry and wet periods that can be be used to determine activity levels (if the animal was in the water or either flying or nesting) (Shaffer et al., 2005)

- GPS loggers, on the other hand, provide frequent precise location estimates (~4 m accuracy). But they are heavier, need a battery and can react badly to being submerged. (A. E. Burger & Shaffer, 2008)

Seabird foraging location can be integrated with environmental covariates, like SST and [Chl *a*], providing a better understanding of the correlation between seabird foraging movements and environmental variability (Jonsen et al., 2013). Different papers showed how foraging behaviour can be influenced by environmental drivers, and how this influences breeding success and population trends (Bestley et al., 2016; Bool, 2018; Wakefield et al., 2009)

iv. The importance of monitoring seabirds' diet

As mentioned earlier, seabirds are highly placed predators on the marine trophic levels, thus good indicators of the state of the lower levels. And since pelagic seabirds are often associated with specific marine habitat features (Weimerskirch, 2002; Zotier et al., 1999), they can represent very good models for assessing the importance of the oceanographic environment, both from ecological and historical perspectives (Gómez-Díaz et al., 2006). It is good to document the response of seabirds towards spatial heterogeneity of their prey, by monitoring their diet, since it can reflect any changes undergoing in prey assemblages and abundance, which can also be linked to broad-scale atmospheric changes processes, underpinning the relationship between prey and predators. Many methods can be used to identify seabird's prey, which include stomach regurgitation (by stomach flushing), extracting DNA from excrements, collection of regurgitation pellets or through direct observation of prey returned to the colony (Barrett et al., 2007). Unfortunately, those techniques don't allow the determination of diet for a bird which spent extended periods of time at sea (Cherel et al., 2000; McInnes et al., 2016). Preys collected from stomachs during breeding season are also not representative of the adult's diet, as it only reflects what is fed to the chick. What's more, preys collected from stomach samples have usually undergone some degree of digestion before collection, and thus can bias the results (Bowen & Iverson, 2013). Fatty acid analysis, stable isotope analysis and other alternative methods are, due to their capability of identification of long-term trends, used to monitor seabirds' diets (Watanuki & Thiebot, 2018). Fatty acid analysis, although relying on a priori information of the fatty acid signatures of prey, can identify species with no hard parts (shells and bones) and can even indicate relative proportions of the consumed prey (Iverson et al., 2004). Stable Isotope analysis (SIA) can be used to determine the trophic position of the prey, as well as providing the source of the prey (where it was before capture) (Bond & Jones, 2009).

b. Special mating habits

i. Mate and nest fidelity

Seabirds will mostly form long-term pair bonds, lasting a lifetime until one of them disappears (Black & Hulme, 1996). Procellariidae in particular will present a strong mate fidelity during their breeding life (John Warham, 1990). Studies showed that *Calonectris borelis*' s nests are extremely close to one another (Swatschek, 1994). This should create a high number of extra-pair copulation (EPC), thus lowering mate fidelity. However, DNA analysis showed that extra-pair fertilisation, subsequent to EPC, is non-existent, or extremely rare. This study gives proof to the very high mate fidelity of this species.

Other studies showed that not only mate fidelity, but also nest-site tenacity had an important role on the reproduction success of Cory's Shearwater (Thibault, 1994). Even if he noted a slight difference in nest fidelity between sexes (84.3% of males, 75.7% of females, kept the same nest site from year to year), he insists on the importance of nest fidelity. Researchers explained that shearwaters have a high natal philopatry, and a high nest site fidelity (Rabouam et al., 1998). A later study showed that divorce rates in the Cory’s shearwater are very low, and that individuals will change mates almost only if the other mate is absent during the breeding period (Mougin et al., 2000). A change of mate or nest can also arise after a reproductive failure, e.g., in case of high predation at the nesting site. New studies showed once again the high nest-site and mate fidelity in procellariiformes (*Hydrobates pelagicus*), where 94% of the studied individuals were faithful to their nest and 95% their mates (Mariné & Cadiou, 2019). Retention of the same nest and mate, from year to year, has two potential advantages for the individuals: 1) the breeding pair will save time and energy at the beginning of the breeding season, not having to find either a partner or a nest, a particularly important aspect for long distance migrants, 2) as they spend much more time together, it may improve the fitness, reproductive success, because of a better coordination between both parents (Thibault, 1994).

ii. Special behaviours

K-strategist species, with long-lived and care-giving parents, individuals are expected to balance the offspring condition with their own. For marine birds, such a balance can be difficult to achieve, namely due to the often-scarce food availability in the marine environment. As the resources available to the parents are limited, both in their distribution in the environment and the time and energy required to obtain them, parents should organise their investment in the offspring and their own self-maintenance, in a way that would balances the costs of their future reproductive success (Gillies et al., 2021; Stearns & Stephen C., 1992; Trivers, 1972).

1. Dual Foraging Strategy and Obesity Strategy

Many species of Procellariiformes display a unique behavioural adaptation to manage such conflicting demands, known as Dual Foraging (Paiva, Xavier, et al., 2010; Tyson et al., 2017). This is because the cost of parental care in terms of reduced parental survival or fecundity are assumed to be high (Linden & Møller, 1989). Dual foraging strategy is used by each individual, in accordance to its own needs. They will alternate long trips and short trips. Long foraging trips (LT) will primarily serve in the adult self-maintenance, even if some food can be brought back to the chick, while the short trips (ST) will solely serve to provision the offspring. For the chick, the adult's short trips represent a great amount of food over a short period, whereas the long trips will represent extended periods of waiting for food, which can affect the chick's body condition, increased starvation during the LT or obesity during ST. This is particularly important when both parents make their LT and ST at the same time. Nevertheless, such a strategy will lead to a prolonged chick growth rate. Thus, it is important for parents to offset their foraging trips so that when one is doing a long, self-maintenance trip, the other makes smaller trips, for the offspring to assimilate food more easily, regularly and develop faster. All-in-all, chick development, growth and thus breeding success of the couple, may be related to how well the trip coordination between both parents was accomplished (Wojczulanis-Jakubas et al., 2018). A study realised that Wedge-tailed Shearwater, *Puffinus pacificus*, will perform short-trips to the nest of durations from 1 to 4 days, followed by a single long trip of ~8 days (Congdon et al., 2005). This tropical species, as well as other more temperate species, will use long trips to replenish their reserves, before fasting during the short trip periods, used solely to nourish the offspring. They also showed that, for this species, the dual-foraging pattern was a consequence of the median time adults require to replenish their body reserves on long trips. In his thesis, Carlos Jorge da Silva Gonçalves (2016) suggested that the return of the mate that just performed a long foraging trip was the cause of the changeover in trips, by interaction with the other mate.

VIII. Studied Species

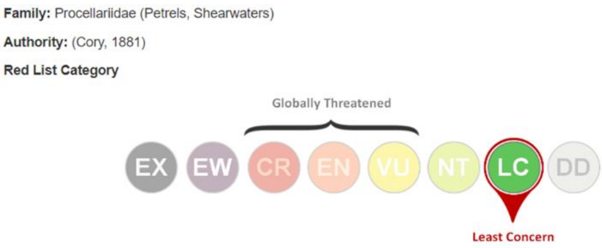
The *Calonectris* species complex comprises Northern subtropical birds, nesting on isolated islands (Gómez-Díaz et al., 2006). The most well-known species of this genus are *Calonectris leucomelas*, the streaked shearwater, from North-East and *Calonectris diomedea.* This last one is now divided into two subspecies, *Calonectris diomedea diomedea*, Scopoli's Shearwater, and *Calonectris diomedea borealis,* Cory's Shearwater (Warham, 1990). Scopoli's breeds along the Mediterranean coasts, while Cory's can be found in the Atlantic. Formerly, *C.diomedea* also had a third subspecies, the endemic Cape Verde Shearwater, *Calonectris edwardsii*, that breeds exclusively in the Cape Verde archipelago. But it is now considered as a full species (Hazevoet, 1995).

In this work we'll be concentrating on two of these species of Procellariiformes birds, *Calonectris borealis* and *Calonectris edwardsii*. Those two species, with similar ecologies, spend most of their time at sea, only going to an in-land nest during the breeding period.

The aim of this study being the understanding of the influence of different environments on the foraging behaviour of the parents, we choose those species for their very distinct habitats. One of them living mostly in the north Atlantic, nesting in the Berlengas archipelago and going sometimes as far as Canada for its Long Trips, the other, the endemic species of Cape Verde, used to warmer and more oligotrophic waters. Those environments, with their own peculiar attributes, will of course shape the foraging behaviour of their inhabitants in different ways.

a. *Calonectris borealis*

Picture by Miguel Rouco, ebird.org



Family: Procellariidae (Petrels, Shearwaters)
Authority: (Cory, 1881)
Red List Category

Figure VIII-1: *Calonectris borealis*

C.borealis has been evaluated as Least Concern according to the IUCN Red List of Threatened Species. It breeds mostly in some islands of the North Atlantic, as Azores, Madeira, Canaries and Berlengas (Paiva, Geraldes, et al., 2010). Considered as relatively common in those areas, the Azores colony, the largest, can harbour up to 188 000 breeding pairs, from which up to 10 524 pairs only on Corvo Island, as seen in 2012 (Oppel et al., 2014). The colony from which our individuals come from is the Melreu colony, a sub colony from the Berlengas Archipelago, where an estimate of 1000 breeding pairs was counted in 2011 and 2015 (Lecoq et al., 2011; Oliveira et al., 2020). Their mating period will extend between April, where the first couples are usually reported to arrive, and November when the last Juveniles leave the nest. It is important to take into account that adults will leave the colony during October, leaving the nestling to themselves during the last month of fledgling.

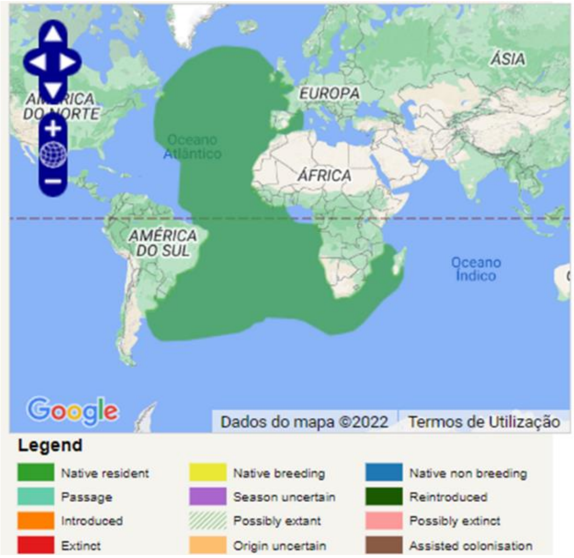


Figure VIII-2: *Calonectris borealis* area of distribution, BirdLife International (http://datazone.birdlife.org/species/factsheet/22732244)

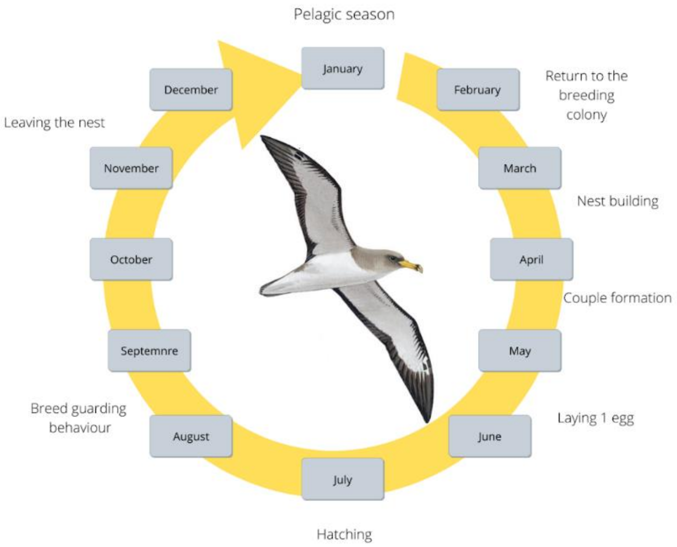
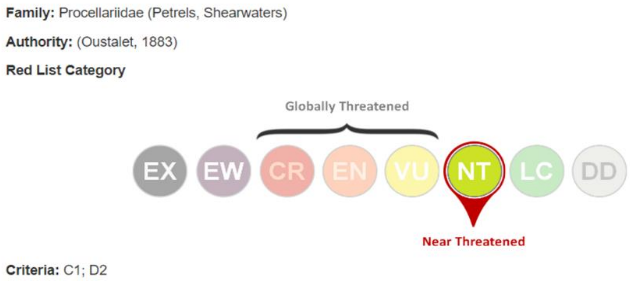


Figure VIII-3: Cory Shearwater's annual life cycle

b. *Calonectris edwardsii*

Figure VIII-4: *Calonectris edwardsii.*



Family: Procellariidae (Petrels, Shearwaters)

Authority: (Oustalet, 1883)

Red List Category

Criteria: C1; D2

C1: a populaion estimated at less than 10 000 mature individuals, due to an estimated continuing decline of at least 10% within 10 years or 3 generations, whichever is longer.

D2: Population with a very restricted area of occupancy or number of locations (5 or lower in general) such that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future, and thus capable of becoming Critically Endangered

C.edwardsii, considered Near Threatened by the 2018 IUCN Red List of Threatened Species, became a very important bio-indicator for the wellness of their environment, and a very studied species. It is now considered locally common in Cape Verde (Hazevoet 1995), and the largest colonies are on islands Raso, Branco and Brava. A full island survey was done during the 2005 breeding season and counted 6312 breeding pairs in Ilheu Raso and 3500 on Ilheu Branco, resulting in a total of circa 24000 individuals. For our work, we studied breeding pairs from the Raso colony for which, more recent works counted an estimated population of ca. 6500 breeding pairs (J. Pereira, 2022).

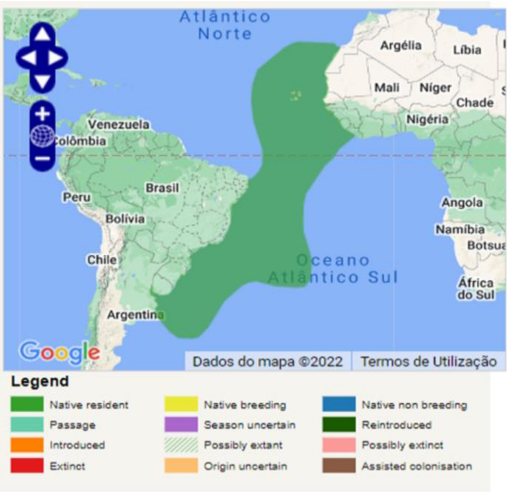


Figure VIII-5: *Calonectris edwardsii* area of distribution, BirdLife International (http://datazone.birdlife.org/species/factsheet/cape-

Both species will have different routes and migratory strategies throughout their lives. Recent studies have shown that the routes and strategies chosen by the birds will evolve throughout their lives (Campioni et al., 2020).

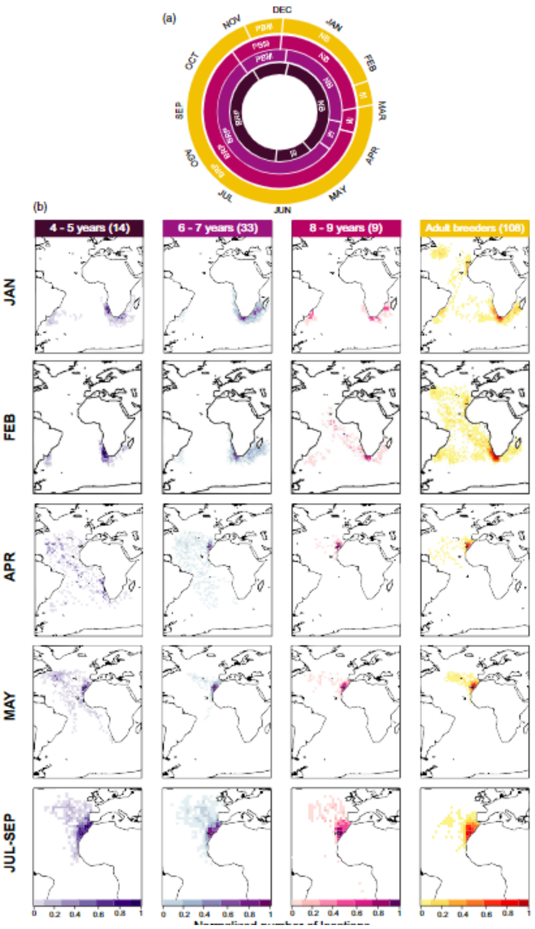


Figure VIII-6: “The annual-cycle scheduels (a) of immatures and breeding Cory’s Shearwaters (BRP: breeding period; M: pre-breeding migration; NB: non-breeding period; PBM: post-breeding migration). (b) A selection of five snapshots is presented to show changes in migratory timings and distributions of Cory’s shearwater according to age and breeding status (JAN: non-breeding period; FEB: adult’s pre-breding migration; APR: immatures’ pre-breeding migration; MAY: pre-laying period; JUL-SEP: breeding period). Data were scaled (Min-Max normalization of number of locations per 1x1 cell) to a fixed range of 0-1. Number of migrations is shown in parentheses.” Campioni et al., 2020

IX. Studied regions

a. Raso Islet, Cape Verde

The Cap Verde archipelago is composed of ten main islands, as well as 13 volcanic islets and some seamounts (Montrond, 2020). Study on their age, locations and characteristics showed that they can be grouped in 3 main alignments (Holm et al., 2008). Raso islets is a part of the central sector of the Northern alignment, along with two other small islands, Santa Lucia and Branco. Raso islet was formed by two main episodes of growth, the lower part older than 2Ma, and the upper one between 0.9 and 1.2 Ma. (Ancochea et al., 2015).

Figure IX-1.a: Geographical location of Raso Islet, Desertas Islands Natural Park, Cabo Verde. (http://avesdecaboverde.blogspot.com/p/cabo-verde)

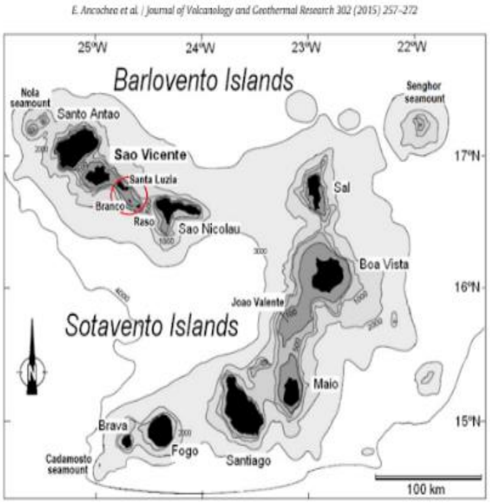


Figure IX-1.b: Location and bathymetric map of the Cape Verde Islands (Ancochea et al. 2010, modified after Holm et al. 2008).

Due to the lack of resources and the very small size of the islet, Raso is one of the last inhabited islands of Cape Verde (Oksana Tariche Pastor et al., 2012). With Branco and Santa Luzia Island its part of an integral reserve, *Reserva Natural Integral de Santa Luzia* (Reservas Naturais, Decreto Lei 3/II/03 de 24 de Fevereiro) since 1990, it is also a protected area on its own (reservas Naturais, Decreto Lei 97/III/90) (Almeida, 2014) and has been identified as an Important Bird Area (IBA) by BirdLife International. *C. edwardsii* individuals we followed all came from the same colony, the largest one in Cape Verde, based on Raso Islet (16º37’0’’N, 24º32’37’’W). The African West coast has several strong currents passing, changing regularly the composition and productivity of its waters. The Cape Verde archipelago zone is between two of those currents, the North Equatorial current, coming from the Canary currents, and the Recirculation gyre, a zone now named the Cape Verde Frontal Zone (Lathuilière et al., 2008). During October, a period of time when *C.edwardsii* is still present at the colony, the sea surface Chlorophyll-a concentration will gradually increase, until it abruptly drops in May. This means that during the fledging period of the young, the waters surrounding the islet will be oligotrophic, with low concentration of nutrients. The closest area with a high productivity will then be the Northwest African Coastline, due to a strong coastal upwelling (Wooster et al., 1976).

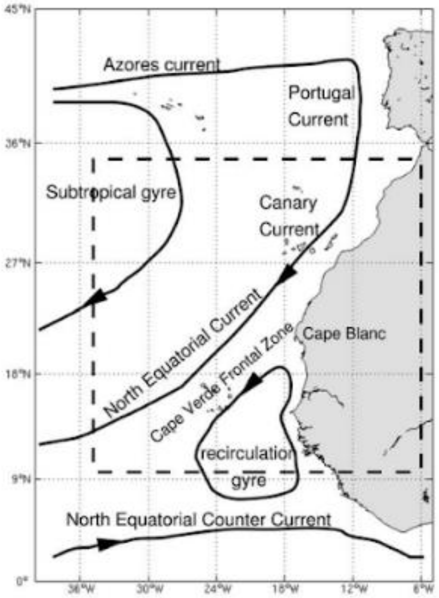


Figure IX-2: "Large scale circulation (adapted from *Mittelstaedt* [1991] and *Stramma et al.* [2005])" Lathuilière et al. 2008

b. Berlenga Island, Portugal

Based 16 km off of Peniche, on the West coast of Portugal, the Berlengas Archipelago is a group of small islands and islets. Berlenga Grande is the biggest and only human populated island, then Estelas, a group of 18 small rocks, and Farilhões, with the highest point, Forcadas (94m). Those formations correspond to Precambrian (538 ± 1 million years ago) emerged submarine mountaintops, the main one presenting an "endemic" mineral -the "Berlengas Granite"-, a coarse-grained red granite, testifying of an ancient boungin of the Gondwana continent, before it splits and formed Europe and America (Azevêdo et al., 2009). The underwater landscape features of this region is quite unique even at an European level. Located near the Nazaré Canyon, one the deepest canyons of the "Gouf " type, 300km from shore, 227 km long, starting at 50m deep and reaching 5000m, in the Iberian abyssal plain (Azevêdo et al., 2009). This dramatic landscape can explain the ecological characteristics of the region, as it interacts with the circulation associated with

Coastal upwelling, thus enriching the surface waters in nutrients and intensifying the primary production phenomena of the ecosystem (Vanney & Mougenot, 1981). This colony is on a neritic system, the island being situated within a long continental shelf of ≤200m.

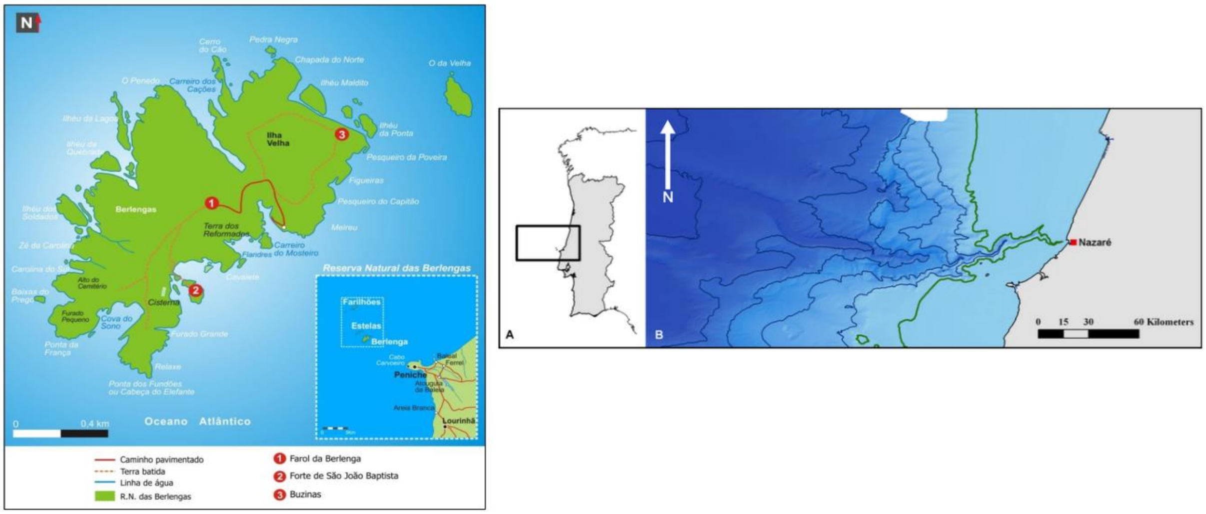


Figure IX-3: Geographical map (www.icnf.pt) and bathymetry map of Berlenga Island, Berlenga Nature Reserve, Portugal (39º24´N, 9º30´W).

Objectives

Main objective of this work is to understand how several environmental drivers (BAT, OLM, SST, NPP, EPI) and environmental conditions of the colony surroundings influence (1) the coordination between mates in foraging behaviour and chick provisioning and (2) chicks' body condition and fitness at fledging. More specifically, we measured how environmental conditions of colony surroundings and foraging areas, drive the foraging choices of adults and how those choices impact the foraging effort and growth of their chicks.

We expect Cory's shearwater parents to exhibit comparatively higher level of at-sea and at-nest coordination, by timing and coinciding in their colony visits at least once each three or four consecutive short (daily) trips and by using similar foraging areas and habitat characteristics (environmental drivers). This should translate into comparatively higher daily body weight increments of their chicks. In turn, Cape Verde shearwater parents should exhibit lower at-sea coordination, especially during the short forays in the colony surroundings/ within the Cabo Verde archipelago, where availability/ predictability of pelagic prey is comparably lower. Because of this, their chicks should exhibit lower body conditions and more variable growth rate. Foraging on the predictable marine region off west Africa at least once each three or four trips, should buffer and compensate for the higher variability in chick growth, to attain an average weight and wing length at fledging high enough to potentiate juvenile survival during early life. To our knowledge, this study is the first compilation of so many factors, as well as the comparison between different populations, in different environments. It should help better understand how seabird populations may evolve in the following years, as a result of the climate alteration impacting their areas of life.

X. References

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INTRODUCTION

Animals have always been adapting to their naturally changing environment, on different scales. But recently, human-related activities have brought unprecedented environmental changes. Researchers are increasingly documenting anthropogenic activities' impacts on wild animals, mostly on behaviour changes. For many species, the first response to those changes will be behavioural adjustments, which may lead to the emergence or loss of traditions in certain species using social learning as a transmission of learned behaviours (Gruber et al., 2019). Such responses can give time for genetic changes to arise, thus facilitating long term adaptations to the new environmental conditions (Tuomainen & Candolin, 2011). However, they also point out that such behavioural responses may also lead to a decrease in the overall populational fitness, as those changes will concentrate on the welfare of the individual rather than the population. Even though they are important for immediate survival, behavioural responses are not always adaptive, nor is behaviour plasticity always sufficient to counter the magnitude of some environmental changes (Wong & Candolin, 2015).

By being extremely diversified, widely distributed and exhibiting behaviour and social organisation complexity similar to mammals, and yet being easily approachable in natural environments, birds have always been excellent subjects in biology, and a keystone in the evolution of ethology (Konishi et al., 1989; Turner, 2007). Marine birds in particular are extremely good bio-indicators of their environment, as top predators and somehow ubiquitous (J. Burger & Gochfeld, 2004). Due to the harsh environment they live in, seabirds usually form long-term pair bonds (Black & Hulme, 1996). As the availability of resources in their colony surroundings may vary, parents should organise their investment between the offspring's care and their self-maintenance, without jeopardising their future reproductive success (Gillies et al., 2021; Stearns & Stephen C., 1992; Trivers, 1972). Breeding pairs may then benefit from coordinating their caring activities (protection of the nest, incubation of the egg, chick provisioning, among other activities) in order to bring the cost-to-benefit ratio of the pair as a whole to a minimum (Gillies et al., 2021). This is particularly true for seabirds, the competing demands of provisioning and self-care being very stark, as the parents usually will feed at more distant foraging sites than the immediate surroundings of the breeding grounds. To solve this issue many procellariiform species display a ’dual foraging behaviour’ (Paiva, Xavier, et al., 2010; Tyson et al., 2017). Parents will then alternate long (LT) and short (ST) foraging trips, in accordance to their own need. LT will serve for the adult self-maintenance, while ST will solely serve to provision the offspring. Several studies (John Warham, 1990; Swatschek, 1994) proved the existence of this behaviour in both *Calonectris borealis* and *edwardsii*. Recent studies suggested that the chick development and growth, thus the breeding success of the couple, is directly related to how well the trip coordination between parents was accomplished (Wojczulanis-Jakubas et al., 2018).

The benefits of pair coordination have already been discussed and confirmed in many species (Tyson et al., 2017; Wojczulanis-Jakubas et al., 2018), but we are still lacking the understanding on what exactly triggers such coordination. Studies suggest that a physical interaction between the parents is necessary in order to keep the coordination to a maximum potential (Gillies et al., 2021), or that the parents base their efforts on the begging behaviour of the chick (Gillies et al., 2021). This would show a certain level of plasticity of the foraging behaviour (Cerveira et al., 2020b), for each individual, in order to adapt their behaviour to external cues. (Grissot et al., 2019) also showed that environmental drivers have an impact on the foraging behaviour of certain species.

Unfortunately, data on this matter is still lacking. Grissot et al. (2019) concluded their study by stating that, even though it is highly probable that environmental drivers impact the foraging behaviour of breeding pairs, it is still uncertain to which degree, and to which extent the coordination is a plastic response of parents to the foraging environment. They affirm that the range of environmental variation could still be below a critical threshold of extreme conditions that would trigger more pronounced modifications of parental foraging patterns and coordination (Grissot et al., 2019). Most studies on the subject have been done on temperate or arctic environment, and only recent studies tackle this problem in tropical environment (Cerveira et al., 2020b), trying to fill the gap in knowledge surrounding those areas.

MATERIAL & METHODS

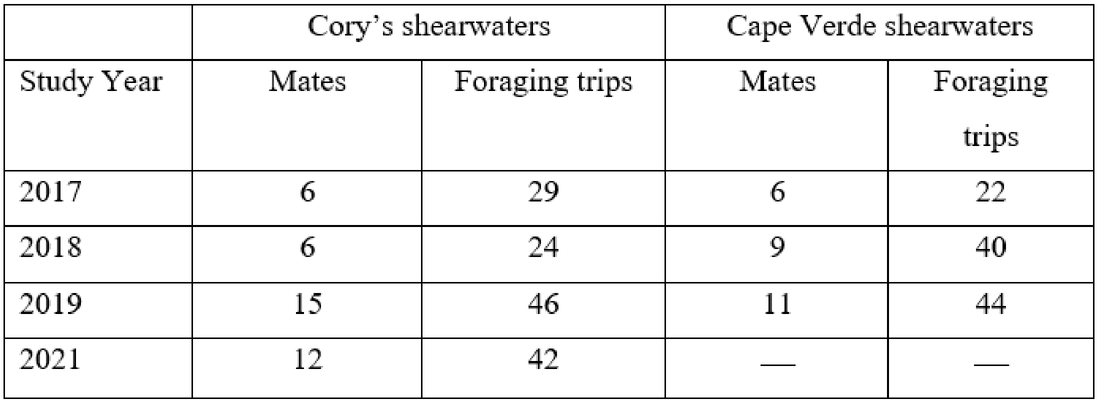
Ethics statement

The deployment of GPS-loggers (see details below) did not take more than 10 minutes and on no occasion did it interfere with reproduction or have visible deleterious effects on study animals. All work on Raso Islet was approved and certified by annual permits (P43_2017, P22_2018 and P21_2019) issued by 'Direcção Geral do Ambiente de Cabo Verde' (DGACV; environment governmental authority of Cape Verde) and work at Berlengas was conducted under permits CAPT_23_2017, CAPT_26_2018, CAPT_42_2019 and CAPT_44_2021 issued by 'Instituto de Conservação da Natureza e Florestas'. All sampling procedures and/or experimental manipulations were reviewed and specifically approved as part of obtaining the field permit.

GPS-loggers deployment and chick growth

Between 2017 and 2021 we have tracked 39 pairs of Cory's shearwaters performing 141 foraging trips and 26 pairs of Cape Verde shearwaters engaging in 106 foraging excursions. (Table XII-1). CatLog2 devices (Perthold Engineering LLC) were attached to the four central tail feathers of both Cory's and Cape Verde shearwaters. Devices were secured using Tesa1 tape, programmed to record locations every 5 minutes, and retrieved 7 – 15 days after deployment. Devices always weighted less than 3% of the birds' body weight to avoid potential deleterious effects on the foraging performance and/ or distribution related with the logger loading (Phillips et al., 2003). At logger retrieval, data on body mass was collected to assess individual body condition. Bird handling time did not exceed 10 minutes to avoid added stress to the animal. Chicks of instrumented parents were weighed (to the nearest 2 g) every 2 days while their parents were being tracked to estimate their mean daily mass variation.

Table XII-1. Number of mates and forays of tracked Cory's and Cape Verde shearwaters.



	Cory's shearwaters		Cape Verde shearwaters	
Study Year	Mates	Foraging trips	Mates	Foraging trips
2017	6	29	6	22
2018	6	24	9	40
2019	15	46	11	44
2021	12	42	—	—

Characterization of adults' at sea behaviours

To define individual behavioural modes from movement trajectories of foraging trips we used the Expectation Maximisation binary Clustering (*EMbC*) R package (Garriga et al., 2016). This is a robust non supervised multi-variate clustering algorithm leading to meaningful local labelling of each GPS location that can be easily linked to biological interpretations (Louzao et al., 2014). Two input variables (speed and turn angle) are used from successive individual locations to assign four behaviours by the *EMbC* algorithm: high velocity/low turning angle (HL), high velocity/high turning angle (HH), low velocity/low turning angle (LL) and low velocity/high turning angle (LH) (de Grissac et al., 2017). Following (Garriga et al., 2016), the behaviours were described as: (1) Resting, when locations show low speed and low turn value (LL), indicating that the bird is resting at the sea surface; (2) Intensive foraging, representing Low speed while searching and High turn value (LH), when patches of prey are spotted; (3) Travelling, showing High speed and Low turn value (HL); and (4) Relocating, reflecting High turns at High speed (HH) as a change between restricted areas of intensive foraging. This technique has been previously used to interpret ecologically meaningful behaviours from movement data in coastal and pelagic seabirds (Lerma et al., 2020; Mendez et al., 2017) including both Cory's and Cape Verde shearwaters (Pereira et al., 2022).

We identified all foraging patches that co-occurred in time (5 min buffer) and space using functions from the *sp* package (Pebesma & Bivand, 2005) and measured the distance between mates with the R package *adehabitatLT* (Calenge, 2006; Jones et al., 2018)

Between mates at-sea overlap

The *kerneloverlap* function with Bhattacharyya's affinity (BA) method of the *adehabitatHR* package (Calenge, 2006)was used to compute the overlap between mates while foraging at-sea. The BA Kernel Utilization Distribution (UD) overlap index ranges from 0 (no overlap) to 1 (identical UDs) (Kochanny & Fieberg, 2005). To test if birds' foraging distributions overlapped more than by chance with fisheries' distributions, correlated random walks within the individual home ranges were simulated using the *simm.crw* function from the *adehabitatLT* R package (Calenge, 2006). To generate each random track, we split the real track into two parts: one from the colony to the most distant location and one back to the colony. We generated 50 simulations per real track [after (Hindell et al., 2020), (Reynolds et al., 2021)] which were then combined to estimate the simulated kernel UDs. We then extracted the 50% and 95% kernel UDs for those random tracks (simulated UDs) and measured the overlap with the distribution of their corresponding mates.

Environmental predictors

To characterise the oceanographic conditions which are associated with "intensive foraging" behaviour we extracted (1) bathymetry (BAT, 0.01° spatial resolution, m) and daily composites of (2) net primary productivity (NPP, 0.08°; mg m^{-3}), (3) biomass of micronekton in the epipelagic layer (EPI, 0.08°, g m^{-2}) and (4) ocean mixed layer depth (OML, 0.08°, m). Bathymetry was downloaded from http://ngdc.noaa.gov/mgg/global/global.html while variables 2-4 were obtained from the Cupernicus database (https://myocean.marine.copernicus.eu/) and are generated through the spatial ecosystem and population dynamics model (SEAPODYM; http://www.seapodym.eu). SEAPODYM is a numerical model that uses physical (e.g. sea surface temperate and currents) and biological variables (e.g. primary productivity) to simulate the spatio-temporal distribution of zooplankton and micronekton (2–20 cm) at a global scale (Lehodey et al., 2008, 2010). This model was previously used as a surrogate of the concentration of low and mid-trophic level prey (e.g. mid-water fish, cephalopods and crustaceans) of seabirds and marine mammals

(Green et al., 2020; Virgili et al., 2021) (Miller et al. 2018, Pereira et al. 2022). All oceanographic raster layers were rescaled at a spatial resolution of 0.08 ° prior to the habitat modelling exercises. Environmental predictors were processed with various functions within the *raster* R package (Hijmans, 2020).

Statistical Analysis

We used the Repeatability (*r*) also known as Intraclass Correlation Coeficient (ICC) (Nakagawa & Schielzeth, 2010) to ascertain which individual (1) trip characteristics (e.g. trip duration, max. dist. to colony), (2) spatial ecology (i.e. 95% and 50% Kernel UD overlap), (3) habitat of foraging areas (BAT, NPP, EPI and OML), (4) patterns of colony attendance (mates nest bout duration, proportion of times mates met at colony) and (5) chick growth parameters (mean daily mass variation) of Cory's and Cape Verde shearwaters had most similarity between (1) sexes and (2) the pair in contrast with the other individuals paired randomly. Tests corrected for (1) year, (2) colony, (3) individual and (4) nest (random factors).

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

Generalized Linear Mixed Models (GLMMs) were used to test the effect of (1) sex and (2) environmental predictors (BAT, NPP, EPI and OML) (independent variables) on (1) change in trip duration (h; measured as the difference between the current and the previous foray of an individual bird), (2) distance between pairs while foraging at-sea (m), (3) mates nest bout duration (h), (4) chicks' daily mass variation (g) (dependent variables). Separate models were run for each study species. Multi-collinearity among covariates was assessed using variance inflation factors (VIFs, *AEDForecasting* library in R (Claster et al., 2016), with variables exhibiting a value higher than 3 being excluded from the modelling exercise.

Year, Nest and Bird ID were included as random effects to control for yearly environmental variability and individual effects. Model family was selected after checking the residuals of models with different families and also based on the lower model AICc value (See Table XIII-1). We started running models including all the main effects and interactions, and the best candidate model was selected based on the second-order corrected Akaike's information criterion (AIC). First-order interactions between independent variables were kept if held significant, otherwise they were dropped from the final model (Burnham & Aderson, 2002).

All analyses were performed within the R Environment (Team, 2021) at a significance level of $P<0.05$.

Table XII-2: Generalized Linear Mixed Model (GLMMs) structures used in the analysis testing the effect of (1) sex and (2) environmental predictors (BAT, NPP, EPI and OML) (independent variables) on (1) trip duration (h), (2) distance between pairs while foraging at-sea (m), (3) mates nest bout duration (h), (4) chicks' daily mass variation (g) (dependent variables). Bathymetry (BAT, m), Net Primary Productivity (NPP, mg m^{-3}), biomass of micronekton in the epipelagic layer (EPI, g m^{-2}), Ocean Mixed Layer Depth (OML, cm). Random effect nested structure included in all models: Year/Nest/Bird

Cory's shearwaters	**Parameters**		
Model	**Response**	**Fixed**	**Family**
1	Change in trip duration (h)	Sex+BAT+NPP	Gamma
2	At-sea dist. between pairs (m)	Sex+EPI+OML	Beta
3	Mates nest bout duration (h)	Sex+BAT	Gaussian
4	Chick daily mass variation (g)	Sex+BAT+NPP+EPI	Gamma
Cape Verde shearwaters	**Parameters**		
Model	**Response**	**Fixed**	**Family**
1	Change in trip duration (h)	Sex+NPP+EPI+OML	Gamma
2	At-sea dist. between pairs (m)	Sex+EPI+OML	Gaussian
3	Mates nest bout duration (h)	Sex+NPP+OML	Gamma
4	Chick daily mass variation (g)	Sex+EPI+OML	Gamma

Variables not shown on the fixed effects were dropped from the modelling exercise due to high collinearity (Variance Inflation Factor; VIF>3)

RESULTS

Inter-annual foraging patterns of study species

During chick provisioning, individual Cory’s shearwaters more commonly invested on short forays in the colony surroundings, though they also endured on some pelagic foraging trips to oceanic areas, predominantly towards seamounts located between continental Portugal and the Azores and along the Portuguese coast (Figure 1).

Cape Verde shearwaters also mostly invests in short foraging trips in the surroundings of Raso Islet and within the Cabo Verde archipelago, enduring after few short trips on a long foray to off West Africa, in a clear dual foraging strategy (Figure 2).

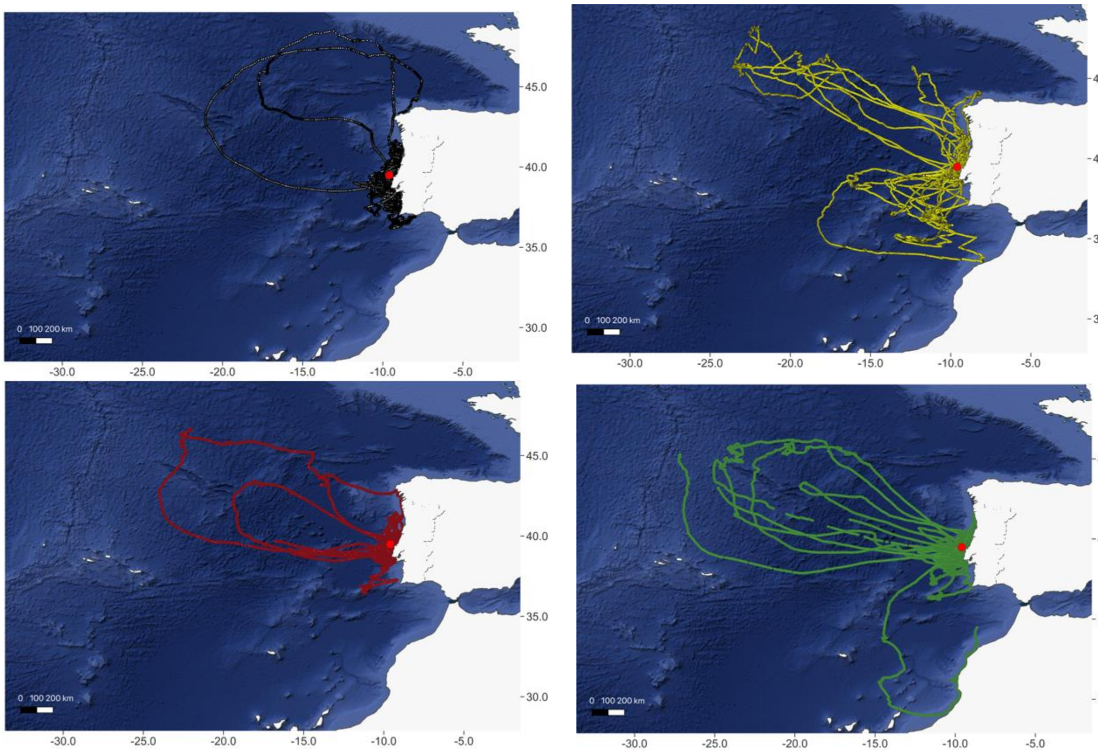


Figure XIII-1: Foraging distribution of Cory’s shearwaters *Calonectris borealis* from Berlenga Island (Portugal) during mid-chick rearing period (mid-August to mid-September) of 2017 (white), 2018 (red), 2019 (green) and 2021 (yellow).

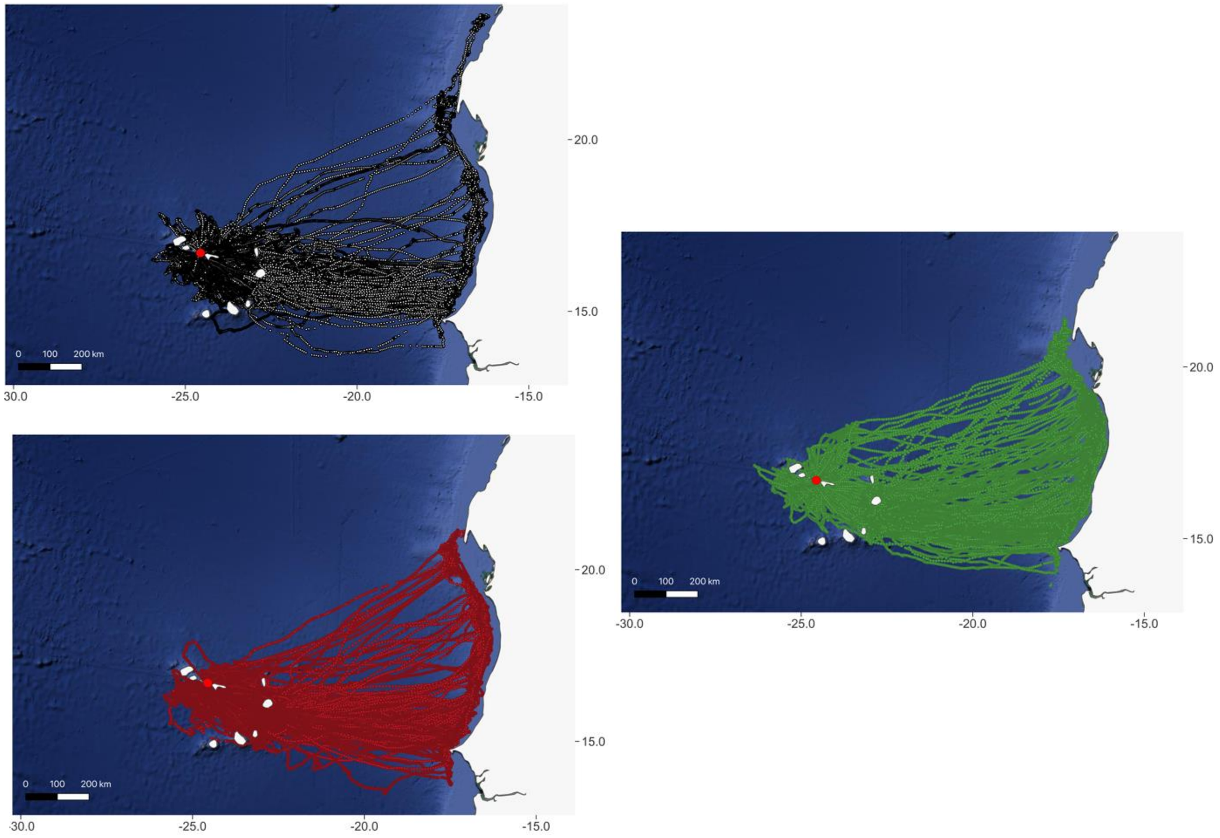


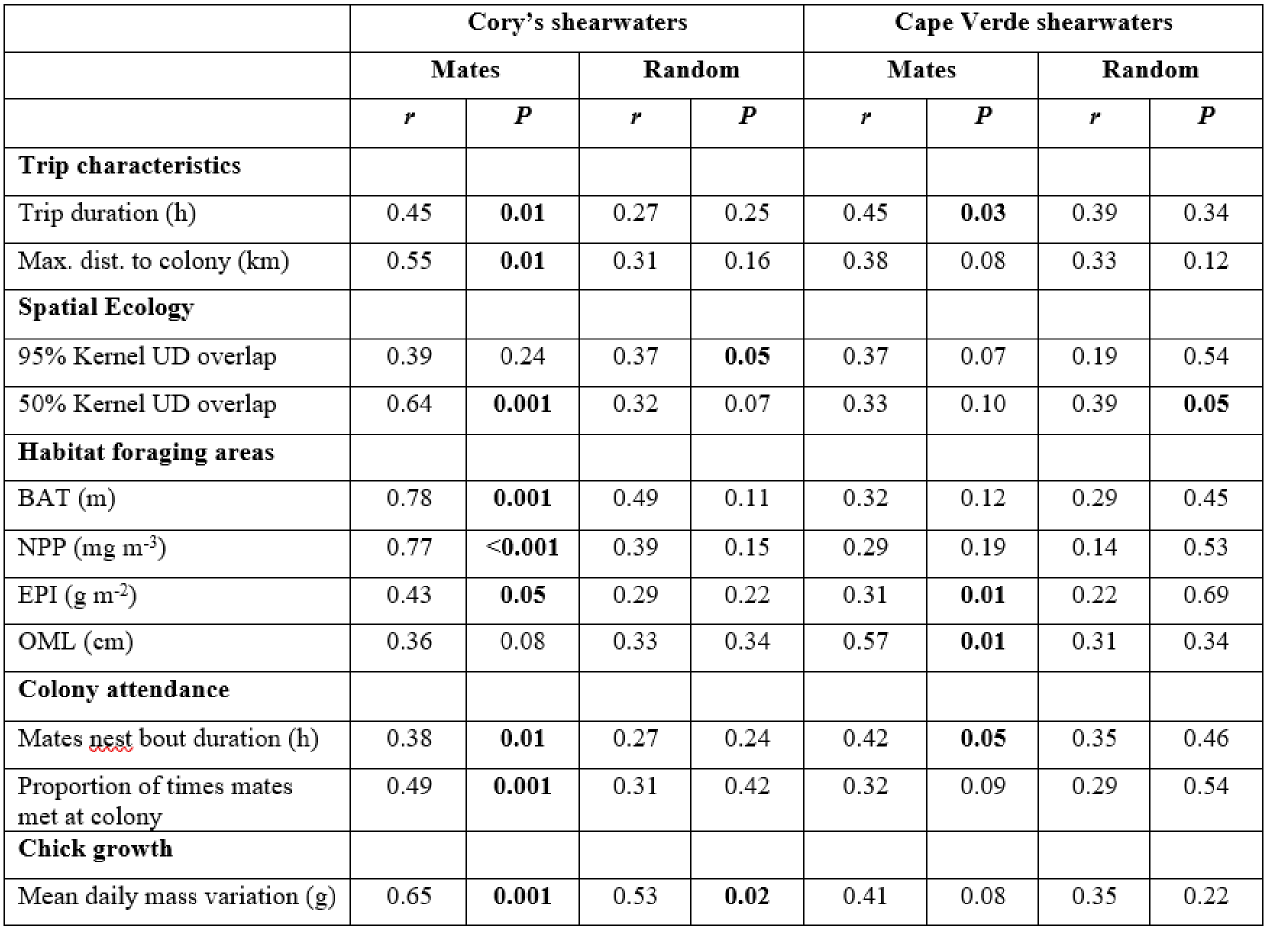
Figure XIII-3: Foraging distribution of Cape Verde shearwaters *Calonectris edwardsii* from Raso Islet (Cabo Verde) during mid-chick rearing period (mid-August to mid-September) of 2017 (white), 2018 (red) and 2019 (green).

Between mates' repeatability in behaviour, spatial ecology and chick growth

Repeatability in trip duration and maximum distance to colony was significantly higher for mates of Cory's shearwaters when compared to randomly assigned mates. Mates of Cory's shearwaters also tended to forage on similar areas (50% Kernel UD overlap) and in habitats with similar bathymetry (BAT), net primary productivity (NPP) and concentration of epipelagic fish (EPI). Mates of this species were also more repeatable in their colony attendance patterns, i.e. nest bout duration and proportion of times meeting at the colony, while their growing chicks had a significantly more repeatable daily mass variation. This was true for both chicks from study nests and random chicks at the colony (Table 2).

Cape Verde shearwaters in their turn, showed only significantly higher repeatability between mates the by chance on trip duration and concentration of epipelagic fish and ocean mixed layer depth of their foraging habitats (Table 2).

Table XIII-1: Repeatability (*r*) and associated P-value in foraging and trophic ecology parameters within mates and among random individuals of Cory's and Cape Verde shearwaters. Pairs of mates or random individuals were always established between male and female. Tests corrected for Sex (fixed factor), Year, Individual and Nest (random factors). Bathymetry (BAT, m), Net Primary Productivity (NPP, mg m^{-3}), biomass of micronekton in the epipelagic layer (EPI, g m^{-2}), Ocean Mixed Layer Depth (OML, cm). Significant results in **bold**.



	Cory's shearwaters				**Cape Verde shearwaters**			
	Mates		**Random**		**Mates**		**Random**	
	r	***P***	***r***	***P***	***r***	***P***	***r***	***P***
Trip characteristics								
Trip duration (h)	0.45	**0.01**	0.27	0.25	0.45	**0.03**	0.39	0.34
Max. dist. to colony (km)	0.55	**0.01**	0.31	0.16	0.38	0.08	0.33	0.12
Spatial Ecology								
95% Kernel UD overlap	0.39	0.24	0.37	**0.05**	0.37	0.07	0.19	0.54
50% Kernel UD overlap	0.64	**0.001**	0.32	0.07	0.33	0.10	0.39	**0.05**
Habitat foraging areas								
BAT (m)	0.78	**0.001**	0.49	0.11	0.32	0.12	0.29	0.45
NPP (mg m^{-3})	0.77	**<0.001**	0.39	0.15	0.29	0.19	0.14	0.53
EPI (g m^{-2})	0.43	**0.05**	0.29	0.22	0.31	**0.01**	0.22	0.69
OML (cm)	0.36	0.08	0.33	0.34	0.57	**0.01**	0.31	0.34
Colony attendance								
Mates nest bout duration (h)	0.38	**0.01**	0.27	0.24	0.42	**0.05**	0.35	0.46
Proportion of times mates met at colony	0.49	**0.001**	0.31	0.42	0.32	0.09	0.29	0.54
Chick growth								
Mean daily mass variation (g)	0.65	**0.001**	0.53	**0.02**	0.41	0.08	0.35	0.22

Intrinsic and environmental drivers of parents' behaviour and chick growth

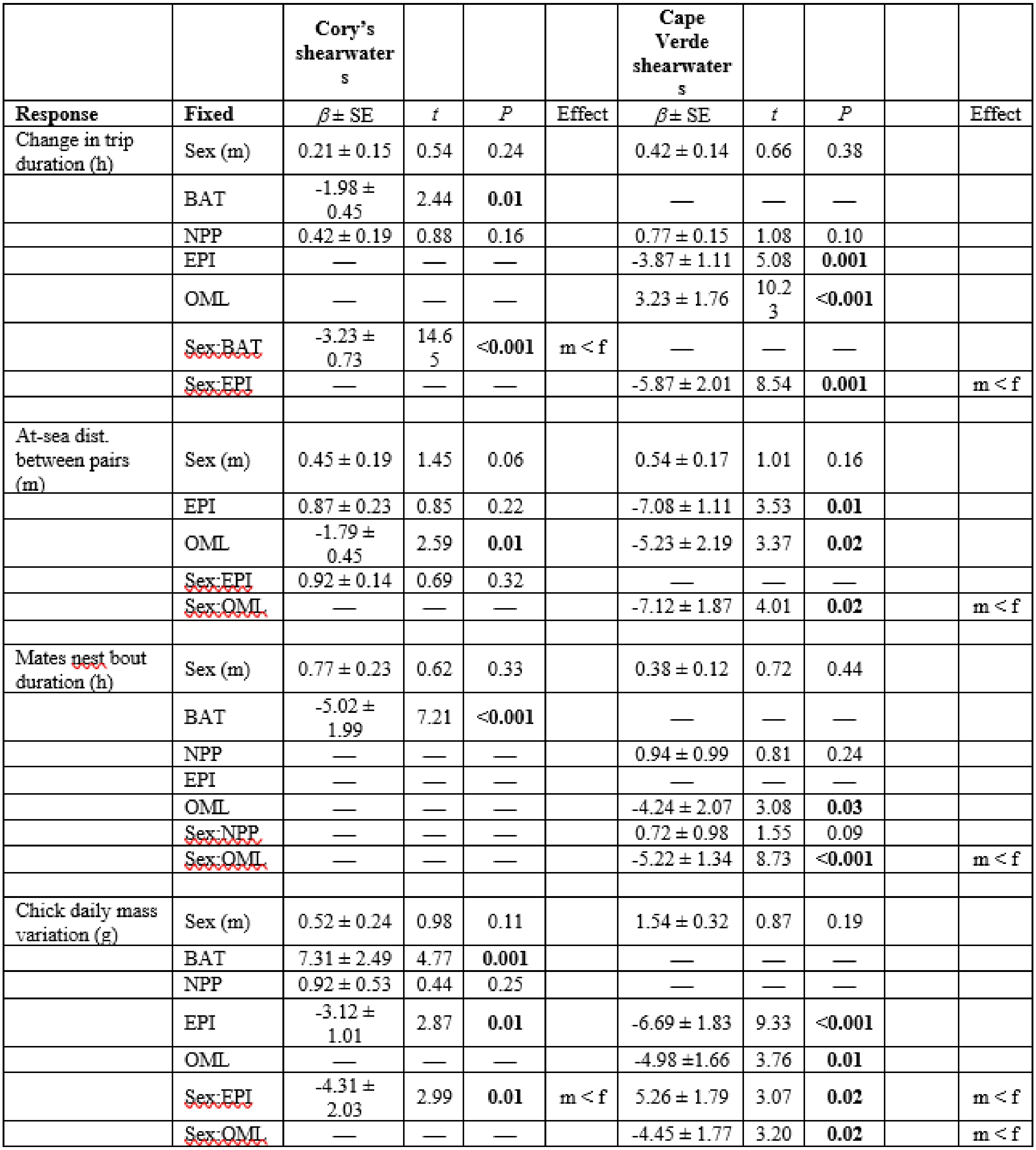
Cory's shearwaters mates showed a decrease in trip duration with increasing bathymetry (BAT) of foraging habitats of their previous trip and there was a tendency for males to react more to these changes in bathymetry when compared to females (Table 3). On the other hand, Cape Verde shearwaters decreased their trip duration with increasing concentration of epipelagic prey (EPI) and decreasing ocean mixed layer depth (OML). Plus, there was a tendency for males to decrease more their trip duration in response to an increase in EPI, when compared to female individuals.

At-sea distance between pairs of Cory's shearwaters decreased with increasing OML from their previous trip, while mates of Cape Verde shearwaters decreased theirs with increasing EPI and OML. The reaction to changes of OML was stronger for male than female Cape Verde shearwaters.

Mates nest bout duration of Cory’s shearwaters mates decreased with increasing BAT of the foraging areas of their previous trips, while for Cape Verde shearwaters it decreased with increasing OML. Once again, male Cape Verde shearwaters seem to react more strongly to these changes in OML when compared to females.

Chick daily mass variation (from one day to another) increased with increasing BAT and decreasing EPI of foraging areas explored by Cory’s shearwater parents, with male parents foraging over lower EPI regions causing an increase on daily mass variation of their chicks. Daily mass variation of Cape Verde shearwater chicks increased with decreasing EPI and OML and this effect was more notorious from the foraging choices of males than females (Table 3).

Table XIII-2**.** Parameter estimates (±SE) from Generalized Linear Mixed Models (GLMMs) testing the effect of (1) sex, (2) environmental predictors (BAT, NPP, EPI and OML) and (3) their interaction (independent variables) on (1) change in trip duration (h), (2) distance between pairs while foraging at-sea (m), (3) mates nest bout duration (h), (4) chicks' daily mass variation (g) (dependent variables) of Cory's and Cape Verde shearwaters. Bathymetry (BAT, m), Net Primary Productivity (NPP, mg m^{-3}), biomass of micronekton in the epipelagic layer (EPI, g m^{-2}), Ocean Mixed Layer Depth (OML, cm). Random effect nested structure included in all models: Year/Nest/Bird. Significant results in **bold**.



		Cory's shearwaters				**Cape Verde shearwaters**				
Response	**Fixed**	*β* ± SE	*t*	*P*	Effect	*β* ± SE	*t*	*P*		Effect
Change in trip duration (h)	Sex (m)	0.21 ± 0.15	0.54	0.24		0.42 ± 0.14	0.66	0.38		
	BAT	-1.98 ± 0.45	2.44	**0.01**		—	—	—		
	NPP	0.42 ± 0.19	0.88	0.16		0.77 ± 0.15	1.08	0.10		
	EPI	—	—	—		-3.87 ± 1.11	5.08	**0.001**		
	OML	—	—	—		3.23 ± 1.76	10.23	**<0.001**		
	Sex:BAT	-3.23 ± 0.73	14.65	**<0.001**	m < f	—	—	—		
	Sex:EPI	—	—	—		-5.87 ± 2.01	8.54	**0.001**		m < f
At-sea dist. between pairs (m)	Sex (m)	0.45 ± 0.19	1.45	0.06		0.54 ± 0.17	1.01	0.16		
	EPI	0.87 ± 0.23	0.85	0.22		-7.08 ± 1.11	3.53	**0.01**		
	OML	-1.79 ± 0.45	2.59	**0.01**		-5.23 ± 2.19	3.37	**0.02**		
	Sex:EPI	0.92 ± 0.14	0.69	0.32		—	—	—		
	Sex:OML	—	—	—		-7.12 ± 1.87	4.01	**0.02**		m < f
Mates nest bout duration (h)	Sex (m)	0.77 ± 0.23	0.62	0.33		0.38 ± 0.12	0.72	0.44		
	BAT	-5.02 ± 1.99	7.21	**<0.001**		—	—	—		
	NPP	—	—	—		0.94 ± 0.99	0.81	0.24		
	EPI	—	—	—		—	—	—		
	OML	—	—	—		-4.24 ± 2.07	3.08	**0.03**		
	Sex:NPP	—	—	—		0.72 ± 0.98	1.55	0.09		
	Sex:OML	—	—	—		-5.22 ± 1.34	8.73	**<0.001**		m < f
Chick daily mass variation (g)	Sex (m)	0.52 ± 0.24	0.98	0.11		1.54 ± 0.32	0.87	0.19		
	BAT	7.31 ± 2.49	4.77	**0.001**		—	—	—		
	NPP	0.92 ± 0.53	0.44	0.25		—	—	—		
	EPI	-3.12 ± 1.01	2.87	**0.01**		-6.69 ± 1.83	9.33	**<0.001**		
	OML	—	—	—		-4.98 ±1.66	3.76	**0.01**		
	Sex:EPI	-4.31 ± 2.03	2.99	**0.01**	m < f	5.26 ± 1.79	3.07	**0.02**		m < f
	Sex:OML	—	—	—		-4.45 ± 1.77	3.20	**0.02**		m < f

Discussion

In general, behaviours of Cory's shearwaters mates were highly repeatable. Knowing that the environment surrounding the Berlengas archipelago is a neritic zone, known for its shallow and productive waters (Santos et al. 2007), with usual enhanced recruitment of pelagic fish (Santos 2001) and persistent and overall biodiversity levels (Gomes et al. 2018), we would expect mates to forage in the colony surroundings, likely repeatedly in the same in the same areas/ habitats (Pereira et al. 2022c). The fact that the habitat characteristics of foraging areas were highly repeatable for most of the environmental variables confirms this hypothesis. The fact that those Foraging Areas related data are repeatable for the couples and not for the randomly paired individuals brings the question of coordination. Studies have shown that a higher degree of coordination in a couple would mean higher fitness (Grissot et al. 2019). For instance, in Little Auks *Alle alle*, parent's body mass increased after a long trip and decreased after subsequent short forays, and researchers have found that coordination between mates was used to minimize such body mass decrease while assuring regular chick provisioning (Welcker et al. 2009). The fact that couples in particular will go to the same foraging areas hints that there is some kind of communication between them, to know those areas, and thus a good coordination. Such "discussion" has been shown to happen as a group behaviour in different species of marine birds (Weimerskirch et al., 2010), such as the Cape Gannets, *Morus capensis* (Courbin N., et al., 2020). This hypothesis is confirmed by the very high repeatability of the colony attendance for Cory's shearwaters' mates. Spending more time together has been showed to bring out better understanding of each other, and thus a better coordination. Studies have shown that longer pair bounds are likely to improve the reproductive performance of the mating pair. In Blue-footed booby (*Sula nebouxii*), an increased pair bound duration would not only increase the individual fitness, but may also create a synergistic effect, for the behaviour of the pair, generating a mate familiarity effect (Sánchez-Macouzet et al. 2014). This being directly linked to the time the pair spends together, which should enhance pair coordination.

Results showed that bathymetry (BAT) seem to be the most relevant environmental driver of behavioural changes in Cory's shearwater mates. This, and the fact that OML wasn't as repeatable as other environmental predictors, should be a result of the environment surrounding Berlengas. Being a neritic habitat, this area will have comparably lower temperature difference between the top water layer and deeper strata, thus having a very weak to no thermocline transition, for which the ocean mixed layer depth (OML) is a good indicator. This will lead to a usually productive upper layer, and thus relatively constant availability of food resources for Cory's Shearwaters. We see that if bathymetry of the last visited foraging area is high (deep water), trip duration will only get shorter. This change means both parents will shift onto short trips, around the island, to find food for their growing chick, until it’s satiated, and one of them can go on a long trip to restore its energy budgets (Magalhães et al. 2008, Paiva et al. 2010a).

We also realise that an increase in BAT will lead to a decrease of time spent at the nest. For the same reason as above, since deeper waters are less productive in this zone, the parents will spend more time at sea in order to gather enough food resources for the nestling (Courbin et al. 2020a). This will of course impact the food brought back to the nestling, impact its growth. Thus, as BAT increases, there is a bigger variation in the chick daily mass intake. All those results hint for a high reproductive success, and general high fitness for the couple and its offspring. This affirmation is confirmed by the very high repeatability of the Mean daily mass variation, which shows that the chick will regularly receive a similar amount of food, leading to a constant growth rate, without few starvation or over-feeding moments. Those results confirm earlier studies showing that Cory’s Shearwater will, when experiencing a period of normal food abundance, provision it’s chick more regularly; in shorter and repeatable intervals (Granadeiro et al., 1998).

Looking into the results, only EPI and OML of foraging areas were highly repeatable between mates of Cape Verde shearwaters. Hence, it is clear that those two environmental drivers hold a significant role in the behaviour of the species. EPI and OML will impact every aspect of the behaviour that we studied, and with much heavier weight that they had for Cory’s shearwaters mates’ behaviour. In this tropical environment, the marine habitats surrounding the colony (within the Cabo Verde archipelago) usually exhibit warmer top layer waters, with a strong thermocline and as such very little mixing with the colder and more productive deeper water (van Pinxteren et al. 2020). This will likely result prey abundance and availability for seabirds (Pereira et al. 2022c). A change in the OML could greatly impact food availability, as a reduced mixed layer would allow better mixture and travel of nutrients from bottom to top of the water column (Bacha et al., 2017; Thiaw et al., 2017). Such changes in the OML are not readily predictable, thus Cape-Verde shearwater individuals must be able to adapt to shifts in prey availability derived from them, as soon as possible. We see that an increase in OML, will immediately increase trip duration, and reduce the time parents will spend at the nest/ colony. This meaning, a higher OML likely translates into low food availability and spend more time at sea than at the colony, reducing the possibility for meeting and thus of coordination. Our results also show that Cape-Verde shearwaters are very dependant of the EPI data, i.e. the nekton concentration in the epipelagic zone.

Data showed a general negative correlation between OML and EPI, as one decreases, the other has a tendency of increasing, which is understandable with the mixing of waters explained above. But since they both entered the regression models, and thus were not highly collinear, we assume other factors might drive those values. Indeed, studies have shown that seabirds from tropical regions, will have positive interactions with other underwater marine top predators, as cues for the presence of prey and/or even to bring prey items back to the surface, known as a “facilitated foraging behaviour” (Veit and Harrison 2017). Indeed, some tropical seabirds are known to be almost exclusively forage in association with Delphinidae schools (Thiebot and Weimerskirch 2013). When those predators hunt, they congregate and push preys to the surface, increasing EPI, and allowing seabirds to have an easier access to prey items, without a change in the OML. All those factors explain why only EPI and OML have shown to significantly influence between mates’ repeatability and overall mates’ behaviour.

Marine tropical areas are known to be oligotrophic environments. With the ever-changing conditions, low productivity, and generally scarce food resources, seabirds in those regions must be quick witted in order to adapt as quickly as possible and prey enough items for them and their chick (Paiva et al. 2015). As each individual must be able to adapt, on its own, to stochastic changes in its environment, coordination between pairs will be very difficult to achieve. The low repeatability of behaviours we obtained on Cape Verde shearwaters inhabiting a tropical realm are proof of this. Even with trip duration being repeatable, the comparably low repeatability on maximum distance to colony shows that every individual will decide where to forage, and not go to the same previously exploited foraging areas, as was the case for Cory’s shearwater mates foraging on the temperate environment. Low repeatability in the nest attendance only strengthens this hypothesis, as it has been shown that mates of some procellariform species achieve a good coordination with regular meetings at the colony (Tyson et al. 2017). In their study of Rhinoceros Auklets (*Cerorhinca monocerata*), Kubo et al. showed that mates will display a high *meeting* phase/ duration at the colony, when compared to randomly assigned hypothetical couples. They suggested that meeting at the nest site regularly would increase the synchronisation of parents (Kubo et al., 2018). Plus, we can see than not only the mean daily mass variation of Cabo Verde shearwater chicks is far from repeatable, but it is extremely linked to the variation in EPI and OML. This shows that those nestling receive very un-regular food intakes, depending on the environmental conditions and what the parents manage to bring back to their growing chick. They will then be submitted to overfeeding, in order to survive the possible long fasting periods. The obesity strategy is known to be employed by many procellariiform species (e.g. *Puffinus tenuirostris* (Hamer et al. 1997) or *Puffinus puffinus* (Hamer and Hill 1997)) when food availability might shift in abundance and availability (Hamer et al. 1997, 1999; Phillips and Hamer 1999), though this is naturally stressful for the chick (Hamer et al. 1997). In fact, although this is an adaptative strategy implied by parents to increase the likelihood of chick survival (Riou and Hamer

2010), the variability in chick provisioning that chicks endure negatively impact its fitness at fledging and adult life. As such, some species have evolved to not use it, as the Northern Fulmar (*Fulamris glacialis*) who's nestling will be fed unusually regularly, and in large quantities, translating into a comparably quicker development (Phillips & Hamer, 2000). Cory's Shearwater, which usually feeds its chick more regularly, might be on the evolving path to also abandon this stressful strategy. However, it is showed that in case of low food resources, they will switch to the "Obesity strategy" (Granadeiro et al. 1998).

In both seabird species, males had a tendency of reacting in a stronger way to environmental changes when compared to female individuals. This might be explained by a carry-over energy loss in the females, from laying the egg. In some species, such as the Western Gulls (*Larus occidentalis*), males will feed the chicks more regularity and travel longer distances than females (Pierotti, 1981). Burger (1981) suggests that male monogamous birds will invest more than females in the reproductive effort. This statement goes against the previously suggested lesser investment of males in the reproductive effort in birds (Trivers, 1972). Generating the rather big egg both our study species lay is extremely energy depleting (King 1973), thus we might expect females to need longer time at sea to replenish their energy budgets, even during brooding period. It was previously reported that in early incubation, incubation shifts of male Cory's shearwaters are usually slightly bigger than those of females, likely to let females recover from the effort of previous weeks creating the egg (Paiva et al. 2013). But further fieldwork and studies are necessary to confirm this on the studied species.

Concluding remarks

We can see clear differences in behaviour for both species. Cory's shearwaters, living in a stable temperate environment, with a constant food availability, will exhibit a comparably higher coordination between mates, going to the same foraging areas and their chick growing in a relatively stress-free environment, receiving a regular food intake. This shows a certain level of habit, more than constant adaptation. However, studies show that Cory's shearwater are able to adjust their foraging behaviour to changing environment in the case of extreme changes (Pereira et al., 2020).

Cape-Verde shearwaters on the other hand, will present a lower level of coordination, as each individual must adapt on its own in order to counter the sudden environmental changes that might happen in its foraging areas. This leads to a unregular food supply, a higher level of stress for both the parents and the chick, which might have an impact on their fitness. However, it shows an exceptional behavioural plasticity and potential to adapt to future environmental changes.

Both species showed signs of learning from their environment and adapting to external changes. Cory’s shearwater may rely more on the constant food resources supplied by its environment, but it still has the capacity of adapting if need be. With the up-coming environmental changes, both studied habitats are bound to suffer some modifications, which will impact their fauna. Being very dependant of their environment, sea birds will need to adapt to whatever changes arises. Our study proved that *Calonectris borealis* and *Calonectris edwardsii* are capable of behavioural adaptation, and gave us a better understanding on which environmental factor will impact those species. More field studies are needed to deepen our understanding of these behavioural adaptations, and how changes might impact seabird populations in climate change driven future.

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