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Sexual segregation in spatial and feeding ecology of seabirds

Fernanda Pereira de Felipe

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Fernanda Pereira de Felipe
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Segregación sexual en la ecología espacial y alimentar de las aves marinas

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Doctoral Thesis, 2019

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SEXUAL SEGREGATION IN SPATIAL AND FEEDING ECOLOGY OF SEABIRDS

Segregación sexual en la ecología espacial y alimentar de las aves marinas

Memòria presentada per

FERNANDA PEREIRA DE FELIPE

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“Prezo insetos mais que aviões.
Prezo a velocidade
das tartarugas mais que a dos mísseis.
Tenho em mim um atraso de nascença.
Eu fui aparelhado
para gostar de passarinhos.
Tenho abundância de ser feliz por isso.
Meu quintal é maior do que o mundo”.

Manuel de Barros

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Abstract

Sexual segregation (SS) is a phenomenon that occurs across a wide range of animal species, with sexes segregating in spatio-temporal distribution, behaviour or feeding ecology. For pelagic seabirds, most studies on SS to date have focused on the breeding period, but the extent of SS and implications in relation to environmental conditions and fisheries, and its occurrence during the non-breeding period, remains poorly understood. We aimed to understand the causes and consequences of SS in spatio-temporal distribution, migratory phenology, behaviour and feeding ecology of three closely-related shearwaters: Scopoli's, Cory's and Cape Verde shearwaters (*Calonectris diomedea, C. borealis* and *C. edwardsii*, respectively). We assessed potential sexual differences during breeding (only for Scopoli's shearwater) and non-breeding periods and discussed whether they persist throughout the annual cycle, and their main drivers. Our results revealed that during the breeding period, females of Scopoli's shearwater seem to be outcompeted by males and forced to increase their foraging effort, especially under unfavourable conditions. Furthermore, we tested for sexual differences in fishing vessel attendance and found that males interacted with fishing vessels to a greater extent, profiting from discards more than females. This indicates that SS in foraging strategies of Scopoli's shearwater may lead to unbalanced exposure of males and females to bycatch in the North-Western Mediterranean, which could reduce effective population size and compromise population viability of the species. During the non-breeding period, both sexes of the three *Calonectris* shearwaters share the same non-breeding areas, suggesting competitive exclusion does not promote spatial segregation throughout the annual cycle. Sexual differences in the migratory phenology were subtle for the three species, with males consistently returning earlier to the breeding colonies, and male Cory's shearwaters remaining resident in a larger proportion than females, likely due to sex-specific reproductive roles at early stages of the breeding period. For both breeding and non-breeding periods, sexes consistently feed on different trophic levels, suggesting that sexual differences in diet may persist year-round. Overall, we found consistent differences in foraging movements, migratory phenology, and resource use between sexes, indicating a robust SS during breeding and non-breeding periods in shearwater species.

Resumen

La segregación sexual (SS) es un fenómeno habitual en animales, como consecuencia de diferencias entre sexos en la distribución espacio-temporal, el comportamiento o la ecología trófica. En aves marinas, el estudio de la SS se ha centrado principalmente en el período reproductivo. En cambio, su alcance e implicaciones en relación a las condiciones ambientales, así como su ocurrencia fuera del período reproductivo, han sido menos estudiadas. Nuestro objetivo fue comprender las causas y consecuencias de la SS en la distribución, fenología migratoria, comportamiento y ecología trófica de tres especies emparentadas: la pardela cenicienta mediterránea, cenicienta atlántica y de Cabo Verde (*Calonectris diomedea*, *C. borealis* y *C. edwardsii*, respectivamente). Para ello evaluamos las diferencias sexuales en el periodo reproductivo (en la pardela cenicienta mediterránea) y de invernada, y discutimos si dichas diferencias se extienden a lo largo del ciclo anual. Para el periodo reproductivo, nuestros resultados indicaron que las hembras de pardela cenicienta mediterránea son menos competitivas que los machos, viéndose obligadas a incrementar el esfuerzo de búsqueda de alimento, especialmente ante condiciones ambientales desfavorables. Además, los machos fueron más proclives a interaccionar con barcos pesqueros, haciendo mayor uso de descartes, pero exponiéndose a un mayor riesgo de captura accidental, lo que podría comprometer el tamaño efectivo de la población y su viabilidad en el Mediterráneo noroccidental. Fuera del periodo reproductivo, ambos sexos compartieron las zonas de invernada en las tres especies, indicando que la exclusión competitiva no causa, al menos a escala espacial, SS a lo largo del año. Ambos sexos se

alimentaron en diferentes niveles tróficos, sugiriendo que la segregación trófica persiste a lo largo del año. Encontramos sutiles diferencias en el calendario migratorio, siendo los machos los primeros en retornar a las colonias, y un mayor porcentaje de machos que de hembras de la pardela cenicienta atlántica no migró, probablemente como estrategia ventajosa de cara a las etapas iniciales del periodo reproductivo. En general, encontramos evidencias de SS en los movimientos de búsqueda de alimento, fenología migratoria y ecología trófica, tanto durante el período reproductivo como en el período de invernada en las tres especies de pardela.

Informe del Director

La tesis doctoral de **Fernanda Pereira de Felipe** titulada *"Sexual segregation in spatial and feeding ecology of seabirds"* incluye dos capítulos relativos a la segregación sexual en aves marinas. Como directores de tesis, informamos de que el capítulo titulado "Sexual segregation in the foraging behaviour of a slightly dimorphic seabird: influence of environmental conditions and fishing activity" fue realizado con igual grado de contribución por la autora de la presente tesis doctoral, Fernanda Pereira de Felipe, y por Jose Manuel González de los Reyes, estudiante de doctorado del mismo programa de estudios de la Universidad de Barcelona cuya tesis también es dirigida por Jacob González Solís Bou. Este trabajo será enviado para su publicación a la revista *Journal of Animal Ecology*, compartiendo ambas personas la primera autoría. De igual modo, este trabajo constituirá también un capítulo en la tesis doctoral de José Manuel de los Reyes. En relación a la contribución de cada autor en este trabajo, la doctoranda Fernanda Pereira de Felipe se encargó de la coordinación y el desarrollo del trabajo de campo, los análisis para el sexado molecular de las muestras en laboratorio y el análisis de isótopos estables. El alumno Jose Manuel González de los Reyes desarrolló los diferentes análisis espaciales y estadísticos e implementó el código necesario en entorno de computación R. Ambos doctorandos redactaron conjuntamente el manuscrito presentado como capítulo de tesis.

Barcelona, 10 de septiembre de 2019

Dr. Jacob González Solís Bou

Dr. Raül Ramos Garcia

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Chapter 1

INTRODUCTION

1

Introduction

1.1. Sexual segregation

Sexual Segregation (SS) is a widespread phenomenon among animal taxa, where males and females segregate in distribution, behaviour and/or feeding ecology (Rubin & Bleich 2005). Traditionally, SS has been defined as the differential use of space and/or resources by sexes (Bowyer & Kie 2004, Ruckstuhl & Neuhaus 2005). Later, more complexity involving asynchrony and differential activity patterns between sexes were added in trying to define and explain SS in animals (Conradt 1998, Ruckstuhl & Neuhaus 2000). However, a widely accepted definition of the term still lacks, and different names have been used to define similar processes throughout the last decades (Ruckstuhl & Neuhaus 2005). Furthermore, elucidation of the proximate mechanisms underlying SS are required to evaluate whether differences in activity and use of space between sexes are a cause or consequence of such SS (Barboza & Bowyer 2001, Bowyer & Kie 2004).

SS has been broadly categorized in: (1) spatial or habitat segregation and (2) social segregation. Spatial or habitat segregation occurs when sexes differ in their use of the physical environment (Clutton-Brock et al. 1982) and can result from different responses of each sex to dynamic factors, such as resource availability, predation risk and local environmental conditions (Wearmouth & Sims 2008). Whilst social segregation is the trend for a given sex to aggregate in separate social groups (Villaret & Bon 1995, Bon & Campan 1996), and might emerge from intersexual avoidance or asynchrony in activity budgets, or intra-sexual affinity (Wearmouth & Sims 2008). Both processes of SS are non-mutually exclusive and can co-occur, i.e., habitat segregation could lead to social segregation (Clutton-Brock et al. 1982), whilst social segregation could eventually occur without habitat segregation (Conradt 1999, Ruckstuhl & Neuhaus 2005).

The underlying mechanism driving SS on habitat and social segregation can be related with the degree of Sexual Size Dimorphism (SSD) in many cases, and hence associated with evolutionary implications (Catry et al. 2005, Ruckstuhl & Neuhaus 2005, Wearmouth & Sims 2008). Dimorphism in body size could result in differential nutritional and energetic requirements, reproductive role specialization, differences in foraging habitats and efficiency, predation risk and in social avoidance to the opposite sex, which could lead to size-mediated dominance in feeding territories (González-Solís et al. 2000, Ruckstuhl & Neuhaus 2002, Catry et al. 2005, Wearmouth & Sims 2008). In sexually dimorphic species, differences in proportions of body parts, in particular in feeding structures, may allow males and females to feed on different prey types (Selander 1966, Newton 2008), which might evolve from or towards to niche-partitioning between sexes to reduce inter-sexual competition for food (González-Solís et al. 2000). However, size alone is not sufficient to fully understand the range of mechanisms underlying SS, since many studies also found differences in distribution, behaviour and in the feeding ecology in species without SSD or only slightly dimorphism (e.g. Sims et al. 2001, Ruckstuhl & Neuhaus 2002, Lewis et al. 2002, Pinet et al. 2012).

SS has been widely studied among terrestrial birds, however, relatively little is known about the underlying causes of SS for marine predators, including seabirds. Studies conducted in the marine environment has always been challenging by the problem of assessing at-sea distribution, due to the inherent difficulty in sampling and equipping individuals (Bograd et al. 2010, Ramos & González-Solís 2012, Meier et al. 2017). Until a few decades ago, much of our knowledge about the ecology of seabirds was restricted to the breeding period, since some of these animals breed on land. The development of remote telemetry systems for tracking movements of individuals has extended our understanding about behaviour and distribution into the non-breeding periods (Hays et al. 2004; Ropert-Coudert & Wilson 2005, Wearmouth & Sims 2008). Nonetheless, whilst detailed behavioural and spatio-temporal information is not always available, the aid of tracking studies have been very efficient in documenting SS in seabirds and has been a focus of avian ecology in the last decades.

1.2. Sexual segregation in seabirds

SS in seabirds can occur at various spatial scales, ranging from subtle differences in diet or microhabitat foraging use to broad geographical distributions during the non-breeding period (Catry et al. 2005, Wearmouth & Sims 2008). During the breeding period, birds are constrained to those sex-specific reproductive tasks and, due to central place foraging strategy, most of them restrict their movements returning repeatedly to the breeding site to rear offspring (Weimerskirch et al. 2009a, Shoji et al. 2015). Hence, sex-specific foraging patterns may be conducted by inter-sexual competition (competitive exclusion) for resources close to the colony (Peck & Congdon 2006, Phillips et al. 2011), when the larger sex may exclude the smaller one while competing for the same resources, and consequently force the former one to travel farther distances to obtain food (González-Solís et al. 2000). Alternatively, parental investment may not be equally shared among parents (differential parental investment) during the stages of the breeding cycle and may cause differing energetic or nutritional requirements between sexes, the “energetic constraint” hypothesis (Elliott et al. 2010). Furthermore, differences in morphology (in body and feeding structures), may promote a habitat or niche specialization, which may persist throughout the annual cycle (Selander 1966, Cleasby et al. 2015). During the non-breeding period, seabirds are not constrained by reproductive tasks, and therefore, they can range for many thousands of kilometres to winter in the most productive areas of the ocean (Shaffer et al. 2006, Bost et al. 2009, Egevang et al. 2010). Diet may also differ across periods due to different energy requirements, foraging ranges and methods, and availability of prey. Breeding periods require larger quantities of specific nutrients and more energy content to ensure the chick provisioning (Perrins 1996, Shaffer 2004), while during migration energy intake is invested in the departing or returning to the colonies (Weimerskirch & Lys 2000).

The degree of SSD is considered an important mechanism upon SS in seabirds (González-Solís et al. 2000, Shaffer et al. 2001, Phillips et al. 2004a, Zavalaga et al. 2007, Weimerskirch et al. 2009b), and may be related to the different parental roles of each sex. Male-biased SSD is thought to be a result from sexual selection, as a larger size is advantageous when competing for mates (Morbey & Ydenberg 2001) or territorial defence (Catry et al. 2005, Kokko et al. 2006, Hedd et al. 2014). Instead, in species with female-biased SSD (i.e. reverse sexual dimorphism), larger females might invest more energy for reproduction, produce larger eggs, provide better quality food for the offspring or even defend territories (Weimerskirch et al. 2009a). For example, costs incurred by egg production (Monaghan et al. 1998) or unequal contribution to incubation (Hatch 1990, Creelman & Storey 1991) may lead to females being in poorer condition than males at the onset of chick-rearing, and consequently to the need to allocate more time to self-provisioning than males. However, SS also occurs in species with non-pronounced SSD and in monomorphic seabirds, (Gray & Hamer 2001, Lewis et al. 2002, Peck & Congdon 2006, Elliott et al. 2010, Pinet et al. 2012, Hedd et al. 2014, Ismar et al. 2017) questioning the importance of SSD also for seabird species.

Furthermore, the dynamism of marine environments, and their spatio-temporal fluctuations in prey availability and distribution, and the inherent intra-specific metabolic requirements of each species may affect the spacing or habitat use of males and females differently, exposing sexes to differential threats (Catry et al. 2005, Bugoni et al. 2011). Sex differences in the foraging behaviour and the differential spatial overlap with high-risk fisheries results in sex-biased mortality in several species of seabirds (Bugoni et al. 2011, Jiménez et al. 2016, Gianuca et al. 2017, Cortés et al. 2018). For example, catches of Scopoli's shearwaters *Calonectris diomedea* in longline fisheries in the Mediterranean Sea are male-biased, especially during the pre-laying period in waters surrounding their breeding colonies (Cortés et al. 2018). On the other hand, the differing at-sea distribution of Wandering Albatross *Diomedea exulans* during the breeding period and its overlap with fisheries was associated with the higher adult mortality of females (Bugoni et al. 2011). An imbalance in the sex ratio caused by differential mortality has severe consequences at the population level and broad implications for population fecundity, viability and dynamics (Durell et al. 2001, Phillips et al. 2005, Mills & Ryan 2005).

Therefore, investigating the mechanisms driving how migratory marine animals, and more specifically, sexes exploit their environment differently, and how they deal with seasonal variation in resources are important issues for wildlife management and species conservation (Bugoni et al. 2011, Gianuca et al. 2017, Cortés et al. 2018). Hence, studying the sex-specific habitat use and movements of seabird species may be critical for understanding the putative causes of their decline. Despite the progress in bio-logging technologies in the last few decades, our knowledge of how each sex interact with the environment and their use of resources remains insufficient requiring further investigation on the theme (Catry et al. 2005, Paiva et al. 2017, Pereira et al. 2018).

Box 1. Marine environment and marine top predators

Marine ecosystems are highly diverse, dynamic and heterogeneous environments, in which productivity is controlled by physical and biogeochemical features and processes (Haury et al. 1978). The spatial and temporal variance in such patterns, promotes a heterogeneous distribution of most productive areas in oceans, with high productive waters being mainly located close to shelf edges or coastal upwellings, while open ocean waters tend to be oligotrophic (Barton et al. 1998). However, despite their high productivity, upwelling regions typically present a high-productive season followed by a less-productive one due to temporal fluctuations of the ocean currents (Davenport et al. 2002).

The upwelling areas harbour complex communities with a wide range of trophic levels from primary producers to top predators (Crawford 2007, Jaquemet et al. 2014). Marine resources are patchily and scattered over large areas of the ocean, however, their concentrations tend to be higher in these regions, which may determine top predator's main foraging locations (Hunt et al. 1999, Weimerskirch et al. 2007). Top predator's foraging locations and behaviour, and their reproductive success are thought to reflect the variability occurring in the lower trophic levels of the ecosystem and might indicate the status of the marine ecosystems (Block et al. 2011, Widmann et al. 2015).

To deal with the dynamism of marine environments, top marine predators may alter their foraging grounds and strategies to cope with seasonal changes in resources availability, to fulfil their energetic requirements, according to species dispersal capacity (Ashmole 1971, Crawford 2007, Green et al. 2009). This is the case of migratory marine animals, including seabirds, which depends on multiple regions throughout the annual cycle to find suitable habitats for the different life-history stages, which may maximize fitness (Greenberg & Marra 2005, Newton 2008).

1.4 Overview of methods

Knowledge on the temporal and spatial distribution and feeding ecology and the relationships between at-sea distribution and environmental characteristics of marine animals has improved due to the combination of the deployment of global location sensor devices (geolocators hereafter), Global Positioning System (GPS) devices and Stable Isotope Analysis (SIA). Geolocator data provide us information about the year-round spatial-temporal distribution and at-sea activity patterns of the study species. Geolocators record light intensity every 60 seconds. Downloaded light records are used to determine day length and times of sunrise and sunset, which are then used to estimate latitude and longitude for every 12-hour period (Hill 1994). Thus, it is possible to access two positions of individuals per day with an average accuracy of about 186 ± 114 km (Phillips et al. 2004b). GPS loggers record geographic position at 1-s intervals and with an accuracy of a few meters (median error of <10 m), which can give us detailed information of the foraging trips and behaviour. SIA of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) within consumer tissues provide a powerful method for studying trophic and spatial ecology of marine organisms (González-Solís et al. 2011, Ramos & González-Solís 2012). The use of these ecological markers is based on the fact that primary producers of different regions and ecosystems present different isotopic compositions due to the different fixed nutrients and biochemical cycle used for photosynthesis; Concentrations of ^{13}C and ^{15}N increase throughout trophic levels, with predictable enrichments between the source and the consumer (Peterson & Fry 1987). The values of $\delta^{13}C$ are generally used as source tracers at the base of the food web, i.e., the feeding zone of the organisms (Hobson et al. 1994, Bearhop et al. 2002). In addition, $\delta^{15}N$ values are mainly used as indicators of the trophic position of organisms and have been widely used to calculate trophic levels in various ecosystems (Cherel & Hobson 2007, Newsome et al. 2007). Soft tissues (e.g., blood, muscle) that are continually renewed have isotopic signatures that will provide dietary information on a time scale that depends on their renewal rates. Furthermore, feathers, that are metabolically inert after their synthesis, have isotopic signatures that will reflect the food that was assimilated by organisms during feather synthesis (Hobson & Clark 1992, Ramos & González-Solís 2012). Thus, analysis of predator tissues with differing isotopic turnover rates may allow investigating the diet of wildlife at different timescales (Dalerum & Angerbjörn 2005). For example, by analysing SIA of red blood cells, we could obtain trophic information of about three to four weeks prior to sample collection, while plasma portion informs in a shorter window of about six days, which may allow us inferring habitat/resource use and trophic position concerning the foraging. In the case of birds, by analysing feathers moulted during the non-breeding period, we can infer the feeding ecology of birds during this period when individuals are often inaccessible to researchers using traditional methods (Barrett et al. 2007).

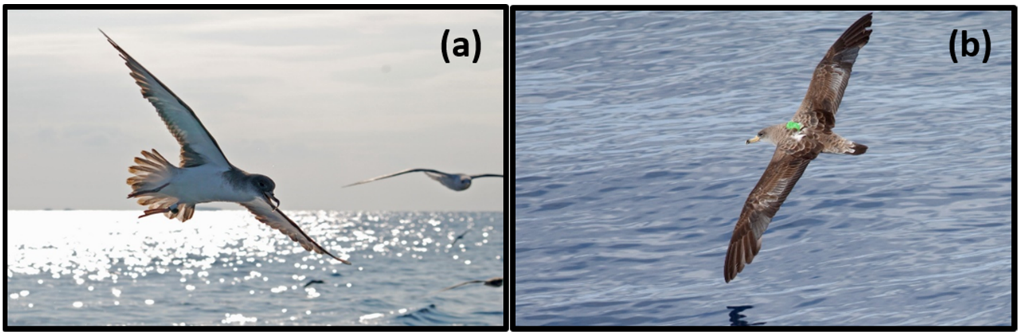

Figure 1. Adult Scopoli's shearwaters *Calonectris diomedea* tagged with tracking devices for this study in the Mediterranean Sea. (a) Shearwater equipped with a geolocator on its left leg; (b) Shearwater with a GPS logger attached to its mantle feathers. Credits: Maties Rebassa (a), Javier Elorriaga (b).

The analysis of both migratory and foraging movements of tracked birds and dietary habits inferred from SIA of blood and feathers have been widely used in studies testing the spatial and feeding ecology of males and females. The year-round investigations of sexual segregation, facilitated by advances in tracking technology, has major implications for our understanding of seabird ecology, because it affects the use of resources, level of intra-specific competition and niche partitioning (Phillips et al.

2017), and can, therefore, provide valuable insights into seabird population dynamics, conservation and management (Catry et al. 2005). For example, differential mortality between sexes is of conservation concern for threatened seabirds such as albatrosses (Mills & Ryan 2005) of which 15 out of 22 species are threatened by extinction (IUCN 2018).

1.5. Study species

Seabirds have been widely used as a study model to understand SS, in particular the family Procellariidae which comprises albatrosses, shearwaters and giant petrels (*Macronectes* spp.), considered as paradigmatic examples of SS in avian ecology (González-Solís et al. 2000, González-Solís & Croxall 2005). Differences in foraging and feeding ecology for both species of giant petrels are related to the SSD, since they are the most sexually dimorphic of all seabirds: males of both species are 16-35% heavier and have disproportionately larger bills than females (González-Solís et al. 2000, González-Solís & Croxall 2005).

Within the Procellariiformes, shearwaters are also well-studied species and much is known about SS in their main foraging areas selected, behaviour and feeding ecology especially during the breeding period (e.g. Navarro et al. 2009, Ramos et al. 2009a, Ramos et al. 2009b, Alonso et al. 2014, Werner et al. 2014, Paiva et al. 2017, Cianchetti-Benedetti et al. 2017). For the non-breeding period, it has been reported that sexes segregate in the migration phenology, behaviour and in the non-breeding areas elected (Catry et al. 2013, Pérez et al. 2013, Müller et al. 2014), including at within-pair level (Müller et al. 2015), but not differed in their feeding ecology (Ramos et al. 2009b, Meier et al. 2017). Furthermore, SSD in wing morphology, body and bill size and shape were considered poor predictors of the way males and females exploit the marine environment in Cory's shearwater *C. borealis* (Navarro et al. 2009, Ramos et al. 2009a).

Calonectris shearwaters are medium-sized long-distance migrants (Thibault et al. 1997, Granadeiro et al. 2006). The genus comprises four species, which are sexually monomorphic in plumage, but show SSD, females being slightly smaller than males in wing length, tarsus length and bill dimensions and having a less robust bill shape (Massa & Lo Valvo 1986, Granadeiro 1993, Navarro et al. 2009, De Felipe et al. 2019). Adults breed mainly on islands and islets, nesting in burrows located on steep coastal cliffs. As other Procellariifomes, *Calonectris* shearwaters lay one single egg per year, and both parents share similar incubation and chick-rearing duties throughout the breeding period (Thibault et al. 1997, Granadeiro et al. 2006). In the present study, we have included three species of the genus:

The Scopoli's shearwater *C. diomedea* is an endemic breeder of the Mediterranean Basin from the Iberian coast to the Adriatic and Aegean (Gómez-Díaz & González-Solís 2007) and it is considered to be a sibling taxon (subspecies or separate species) of the Cory's shearwater *C. borealis* (Sangster et al. 2012). The Cory's shearwater breeds in several islands in the northeast Atlantic Ocean, although the species also breeds in sympatry with Scopoli's shearwater in two colonies in the Mediterranean Sea (at Chafarinas Island and Terreros Islet, close to the Strait of Gibraltar; Gómez-Díaz et al. 2009). The Cape Verde shearwater *C. edwardsii* is endemic to the Cape Verde Islands (Hazevoet 1995). The breeding phenology of the three species is similar in time: birds arrive at the colonies from late February to early March, the laying period begins in the mid-May and chicks start hatching in mid-July. Fledglings usually departure from the colonies from mid-October to early November (Hazevoet 1995, Thibault et al. 1997, Granadeiro 1999). The main non-breeding areas of the three species are located in the

Atlantic Ocean, however, Cory's shearwater present a broader distribution, with some birds wintering in the North Atlantic and the southwestern Indian Ocean (Petry et al. 2000, González-Solís et al. 2007, Müller et al. 2014).

Figure 2. Breeding pairs of the three study species photographed inside their nests. (a) Scopoli's shearwaters at Cala Morell colony in Menorca (Balearic Islands) captured in 2015, (b) Cory's shearwaters at Montaña Clara colony (Canary Islands) in 2008, and (c) Cape Verde shearwaters at Raso islet, Cape Verde in 2008. Credits: Leia Navarro (a), Jacob González-Solís (b), Raül Ramos (c).

Chapter 2

OBJECTIVES

2

Objectives

The main objective of the present thesis is to better understand the causes and consequences of sexual segregation in the feeding ecology, in the choice of main foraging and non-breeding areas, in at-sea behaviour and migratory phenology of *Calonectris* shearwaters during the breeding and non-breeding periods. The referred issues were addressed through a multidisciplinary approach combining geolocation, GPS-tracking and SIA in three closely related shearwater species: the Scopoli's, Cory's and the Cape Verde shearwaters. We believe that studies about behaviour, distribution and feeding ecology conducted with the same species during the breeding and non-breeding periods, could give us important insights on whether sexual differences occur as a result of ecological specialization, which might persist throughout the annual cycle. Furthermore, a multi-specific comparison study conducted with *Calonectris* shearwaters focused on SS during the non-breeding period, has never been conducted as far as we know.

To achieve this aim, we present two chapters with the following specific objectives:

In the Chapter 1, we studied SS in: (1) foraging movements (inferred through GPS-tracking data), in (2) feeding ecology (inferred through SIA), and (3) fishing vessel attendance (inferred through GPS-tracking and Vessel Monitoring System (VMS) information) of Scopoli's shearwaters breeding in the Balearic islands and foraging in the North-Western Mediterranean over four years of contrasting environmental conditions. We expected females to be outcompeted by males, so females will show a segregation in foraging areas and resource use with respect to males, resulting in a greater foraging effort in females. This effect would be exacerbated with an increasing competition, i.e. in unfavourable years with poor environmental conditions (Paiva et al. 2017). Finally, in years with more fishing activity and good environmental conditions, we expected males and females will exploit fishery discards evenly as this resource will be more available, but in unfavourable years competitive exclusion will limit the access of females to discards (Cianchetti-Benedetti et al. 2018).

In the Chapter 2, we evaluated the degree of SS in: (1) the spatio-temporal distribution (inferred through geolocation data), (2) the at-sea behaviour (through immersion data), and (3) the feeding ecology (inferred through SIA), of three closely related shearwaters: the Scopoli's, Cory's and Cape Verde shearwaters during the non-breeding period for six consecutive years. We also evaluated the influence of SSD in bill size on the feeding ecology of each species. We expect that SS in spatial and in feeding ecology would not persist during the non-breeding period, since during this period seabirds are not constrained to reproductive tasks and can disperse hundreds to thousands of kilometres to winter in the most productive areas of the ocean (Shaffer et al. 2006, Bost et al. 2009, Paiva et al. 2010, Egevang et al. 2010), decreasing between-sex competition (Phillips et al. 2011).

Chapter 3

SEXUAL SEGREGATION IN THE FORAGING BEHAVIOUR OF A SLIGHTLY DIMORPHIC SEABIRD: INFLUENCE AND IMPLICATIONS OF ENVIRONMENTAL CONDITIONS AND FISHING ACTIVITY

3

Sexual segregation in the foraging behaviour of a slightly dimorphic seabird: Influence and implications of environmental conditions and fishing activity

Abstract

Sexual segregation in foraging strategies is well known in seabirds, but its extent and implications in relation to environmental conditions and fisheries is little studied. Sexual differences in fishing vessel attendance are of particular concern, since uneven mortalities may exacerbate bycatch impacts. From 2012 to 2015, we tracked 635 foraging trips from 78 Scopoli's shearwaters *Calonectris diomedea* foraging in the North-Western Mediterranean, a region with a strong fishing activity monitored with VMS. We collected plasma samples at GPS recovery for stable isotope analyses. Despite contrasting values of NAO over the four years, shearwaters consistently foraged in the Menorca channel (short trips) and the Catalan waters (long trips). In years with unfavourable environmental conditions, shearwaters increased foraging effort (longer foraging trips in distance and time) and showed a lower fishing vessel attendance, likely due to a decrease in fishing fleet activity and related lower availability of fishery discards. Males showed a lower foraging effort (shorter foraging distances and time), a higher trophic level (higher δ^{15}N values in plasma), a broader isotopic niche width and a higher fishing vessel attendance than females. We also found an increase of δ^{15}N values correlated with fishing vessel attendance, indicating males make a greater use of discards than females. Overall, the sexual differences observed may mostly emerge from differential fishing vessel attendance and consumption of fishery discards between males and females. Despite the slight dimorphism of this seabird species, our results revealed sexual differences in resources use, foraging strategies and fishing vessel attendance, suggesting some competitive exclusion of females from main foraging areas and resources of males, particularly in unfavourable years. This study shows that sexual segregation in foraging strategies can lead to unbalanced exposure of males and females to important threats, which can reduce effective population size and compromise population viability of long-lived species.

KEYWORDS

North-Western Mediterranean · Trophic ecology · Feeding ecology · Seabird-fishery interactions · Diet · Procellariforms

3.1. Introduction

Sexual Size Dimorphism (SSD) frequently drives sexual differences in foraging strategies, which can work as a mechanism to endure or even avoid competition between individuals of opposite sex (Catry et al. 2005). In environments with limited resources, the dominant sex, usually the larger one, gains priority of access to preferred resources by competitive exclusion (Ruckstuhl & Neuhaus 2006). As a result, the smaller sex is forced to shift foraging strategies, which leads to sexual segregation in space, habitat use or food resouces (González-Solís et al. 2000, Phillips et al. 2011). SSD may imply different body size but also different size in structures associated with prey handling, such as the bill, allowing each sex to specialize on different prey type due to variation in foraging abilities (Catry et al. 2005). In such circumstances, diet specialization by sex allows segregation in the trophic niche by resource partitioning rather than spatial segregation (Lewis et al. 2005).

The mechanisms underlying sexual segregation have been explored in many sexually dimorphic species (González-Solís et al. 2000, Phillips et al. 2004, Ruckstuhl & Neuhaus 2006), yet less attention have been paid to species with slight SSD, in which differences in foraging strategies may not only be mediated by body size (Lewis et al 2002, Phillips et al. 2011). Instead, previous findings (e.g. Cleasby et al. 2015, Paiva et al. 2017) suggest that in species with slight SSD, differences are driven by the interaction among SSD, habitat selection and environmental conditions. That is, in some species, sexual segregation is largely driven by habitat segregation, regardless of environmental conditions (Cleasby et al. 2015). In others, in years with low resource availability, males and females feed on different prey items but also use different areas (e.g. Paiva et al. 2017, Soldatini et al. 2019).

In the marine environment, resources are patchily distributed across the oceans, but they are often predictable at large spatial scales (Stewart et al. 2000, Weimerskirch 2007). The extreme vagility of many seabird species allows them to search for prey over hundreds to thousands of kilometres, although in the breeding period birds are constrained by central-place foraging (Spear & Ainley 1997, Paiva et al. 2010). In that period, colonial breeders engage in intense foraging on the feeding grounds within the surroundings of the colony, which can cause local depletion of prey resources, the so-called Ashmole halo (Ashmole 1963) and, consequently, it could also increase inter-sexual competition (Orians & Pearson 1979, Lewis et al. 2001). Competition can also be intensified in unfavourable environmental conditions with prey scarcity (Oro et al. 2004, Paiva et al. 2013). It is expected that, with an increasing inter-sexual competition, individuals of subordinate sex are outcompeted and end up paying higher costs by increasing foraging effort, i.e. expanding and segregating their foraging areas from those of the dominant sex and therefore foraging longer distances and for longer periods.

A particular case of food resource is fishery discards, an easy accesible and predictable resource for many seabird populations, and not available for seabirds naturally (Montevecchi 2002). It is known that the association of seabirds with fisheries can have deep consequences in their biology, modifying foraging movements, diet or breeding success among others (Arcos & Oro 2002, Arcos et al. 2008, Grémillet et al. 2008, Bartumeus et al. 2010). When this important resource is abundant, competition should decrease and the between-sex overlap of foraging niches may increase (González-Solís et al. 1997, Oro et al. 2013). In conditions of discards shortage, however, competition for this resource could increase, leading to less competitive individuals to reduce fishery attendance and rely more on natural prey to avoid competition (Oro et al. 2013, Paiva et al. 2017).

Although the majority of discards are provided by trawlers and to a lesser extent by purse-seiners, seabirds also attend longliners to try to catch the baited hooks, which frequently results in bycatch (Bicknell et al. 2013). Globally, 500,000 seabird are estimated to be killed annually by long-lining, being procellariforms among the most caught groups and thus calling for conservation concern (Rodríguez et al. 2019). Several studies have reported male-biased mortality in bycatch events (Bugoni et al. 2011, Gianuca et al. 2017, Cortés et al. 2018), and found it related to a different at-sea distribution of males and females, instead of differential access to feeding resources related to SSD (Bugoni et al. 2011, Gianuca et al. 2017). Since seabirds are socially and mostly sexually monogamous and adult mortality entails in a pair-bond disruption and related breeding failure, the sex-biased mortality produced by bycatch can drive to a reduction of the effective population size (Mills & Ryan 2005, Weimerskirch et al. 2005).

Here we used a 4-year dataset combining GPS tracking, environmental data, Stable Isotope Analysis (SIA), and Vessel Monitoring System (VMS) information to investigate sexual segregation in the foraging movements of Scopoli's shearwaters (*Calonectris diomedea*). We studied a population breeding in the Balearic islands and foraging in the North-Western Mediterranean (NWM hereafter). We characterized the foraging behaviour, space and resource use, and fishing vessel attendance of males and females over four years of contrasting environmental conditions. In this species, females are slightly smaller and have smaller bill than males (Reyes-González & González-Solís 2016, De Felipe et al. 2019). Studies conducted with this species during the breeding period found that it feeds on a wide range of epi- and mesopelagic fish, such as sardines and anchovies (Afán et al. 2014, Grémillet et al. 2014). Some regions in the Mediterranean are known to encompass major spawning areas of such fish species (Palomera et al. 2007). However, it is also known that their stocks are currently depleted due to the combined effects of climate change and intense overfishing (Papaconstantinou & Farrugio 2000, Coll et al. 2008, GFCM 2017), which may explain the current use of alternative prey by shearwaters, such as fishery discards or krill (Arcos & Oro 2002, Grémillet et al. 2014). In this work, we expected females to be outcompeted by males, resulting in a greater foraging effort in females. This effect would be exhacerbated with an increasing competition, i.e. in unfavourable years with poor environmental conditions.

3.2. Material and methods

3.2.1. Model species and study area

Scopoli's shearwater is a medium-sized, long-lived, pelagic seabird endemic to the Mediterranean, breeding colonially in islands and islets all along the Mediterranean coast during boreal summer (Gómez-Díaz & González-Solís 2007, Reyes-González & González-Solís 2016). Laying starts in the second half of May, and hatching starts in mid-July. Fledgling usually occurs in the second half of October (Thibault et al. 1997, Telailia et al. 2014). Adults breeding in Balearic Islands usually forage over the Spanish Mediterranean waters, from the Strait of Gibraltar to the Cap de Creus (Reyes-González et al. 2017) and often associate with fishing vessels (Arcos et al. 2008). In the NWM, the species represents over 50% of all birds accidentally caught in longliners, with an estimated annual decrease of 4–6% of the local population (Belda & Sánchez 2001, García-Barcelona et al. 2010, Genovart et al. 2018).

Northern cliffs of Menorca Island hold the largest population of Scopoli's shearwater in Balearic Islands, estimated in 1,000–6,000 pairs (Catchot 1992, Martí & Del Moral 2003). Fieldwork was conducted for four consecutive years (2012–2015) during the chick-rearing period (July-September) in Cala Morell (Latitude 40.055º, Longitude 3.869º), on breeders rearing a chick.

3.2.2. Capturing and handling

For deploying and recovering loggers, birds were captured at night, using a looped pole or by hand, when they landed at the colony or once inside the burrow. In order to minimise the possible impact on the breeding success, we did not tag simultaneously both partners of the same couple. Loggers were recovered not earlier than four days and usually earlier than 3 weeks after deployment. Blood samples for molecular sexing and SIA were taken at GPS recovery. All animals were handled in strict accordance with guidelines for ethical research defined by the current European legislation and the University of Barcelona Local Ethical Review Procedures, and under licence approved by respective environmental agencies of Govern de les Illes Balears and Spanish Goverment.

3.2.3. Tracking data

To study the movement and behaviour during the chick-rearing period, we equipped adult breeders with waterproofed GPS loggers (©Perthold Engineering LLC) encased in heat-shrink tube for water proofing. We set the devices to record one location every 5 min (median error of <10 m; Forin-Wiart et al. 2015, Morris & Conner 2017) and attached them to mantle feathers with salt-water resistant Tesa® tape. Total mass of devices (~23 g) was below 4% of adult mass, as recommended by Phillips et al. (2003) and Passos et al. (2010). Overall, we tracked 78 individuals (45 males and 34 females) over the four years period (see Table 1). 47 individuals were tracked only one year, 23 individuals two years, 6 individuals three years and 2 individuals four years.

Table 1. Sexual differences in trip parameters. Regional environmental conditions (NAOw), sample size, and observed annual means (± Standard Deviation, SD) of the trip parameters and related metrics from males and females of Scopoli's shearwaters sampled at Cala Morell (Menorca, Balearic Islands, Spain) between 2012 and 2015. NAOw represents the averaged winter (December–March) North Atlantic Oscillation index scaled. Values are mean ± SD. Fisheries attendance indicates the maximum number of attendance events to fishing vessels. Ratio A/F indicates the mean value of the ratio of the recorded number of attendance events respect to the recorded number of foraging locations within a trip. VMS indicates the daily average of individual fishing vessels operating at each area and in brackets the total amount of VMS locations registered every year within the bird foraging areas and tracking period (excluding locations at harbour). BAL = Balearic waters, CAT = Catalan waters.

	2012		2013		2014		2015	
NAOw	1.04		-1.20		1.60		1.89	
Sex	Males	Females	Males	Females	Males	Females	Males	Females
Individuals (n)	24	20	12	11	14	10	17	12
Trip parameters								
Foraging trips (n)	76	60	117	103	81	52	99	47
Long trips	7	8	13	13	7	18	20	20
Short trips	69	52	104	90	74	34	79	27
Max. distance (km)								
Long trips	238.3 ± 30.4	211.8 ± 30.2	200.9 ± 24.8	211.7 ± 25.2	200.0 ± 15.2	206.6 ± 38.0	203.5 ± 19.5	210.7 ± 24.8
Short trips	47.7 ± 21.0	52.9 ± 24.5	44.1 ± 23.6	44.7 ± 23.9	36.9 ± 18.0	42.4 ± 30.2	49.5 ± 24.5	51.8 ± 29.8
Distance covered (km)								
Long trips	1165.9 ± 485.7	1093.9 ± 615.5	820.3 ± 276.8	808.9 ± 320.1	752.9 ± 193.9	697.7 ± 293.5	734.8 ± 209.4	1043.3 ± 447.3
Short trips	227.7 ± 141.9	266.8 ± 139.8	189.2 ± 153.3	193.8 ± 135.9	165.3 ± 92.7	203.2 ± 140.4	200.4 ± 103.0	236.5 ± 135.1
Trip duration (days)								
Long trips	5.4 ± 2.0	4.8 ± 3.1	3.2 ± 0.9	3.7 ± 2.6	3.3 ± 1.2	2.8 ± 2.0	2.8 ± 1.2	4.6 ± 2.3
Short trips	1.3 ± 1.0	1.6 ± 1.0	1.1 ± 0.9	1.2 ± 0.8	0.9 ± 0.4	1.1 ± 0.7	0.9 ± 0.5	1.1 ± 0.7
Foraging ground size (km^2)								
Single-trip level	491 ± 289	628 ± 509	565 ± 427	528 ± 371	454 ± 277	717 ± 519	641 ± 427	971 ± 668
Population level	6194 ± 1303	8750 ± 1717	8057 ± 1601	7833 ± 1443	6159 ± 1149	11703 ± 1252	9814 ± 1533	14956 ± 880
Behaviour								
% of foraging	53.5 ± 14.4	50.3 ± 16.8	48.8 ± 16.6	48.2 ± 13.6	51.0 ± 14.4	48.2 ± 12.3	49.7 ± 16.5	52.4 ± 13.4
% of relocating	22.4 ± 7.7	21.5 ± 8.8	22.2 ± 10.3	21.3 ± 8.9	23.1 ± 11.9	24.1 ± 9.7	25.2 ± 11.3	26.3 ± 10.4
% of resting	36.5 ± 9.7	39.7 ± 12.1	40.9 ± 13.3	40.0 ± 12.1	44.5 ± 13.3	40.6 ± 10.2	37.3 ± 12.9	37.2 ± 11.9
Fisheries attendance								
Max	7	9	11	16	4	6	9	7
Ratio A/F (x 1000)	0.8	0.7	2.9	1.3	4.1	0.2	1.1	1.3
VMS								
CAT	138 (74504)		166 (344793)		160 (259393)		146 (172891)	
BAL	27 (12955)		32 (79717)		28 (43192)		26 (26020)	

3.2.4. Environmental data

We used different proxies to evaluate the effect of annual environmental variability. Inter-annual variability in the North Atlantic Oscillation Index (NAO) is linked to annual changes in wind patterns, sea surface temperature and rainfall in the North Atlantic, impacting ecosystem dynamics, marine productivity and distribution of prey species (Durant et al. 2004, Báez & Real 2011). Conversely to its effects in the North Atlantic and Western Europe, in the Mediterranean basin negative values of NAO promote an overall increase in the productivity and abundance of marine organisms from lower to upper trophic levels, whereas positive values of NAO lead to resource scarcity (Hurrell 1995, Mann & Lazier 2006, Genovart et al. 2013). In addition, it has been shown that fluctuations during winter directly affect food availability in subsequent months and therefore influence the performance of top predators (Oro et al. 1995, Paiva et al. 2013). Thus, we used the extended annual winter NAO (NAOw hereafter) by averaging the winter monthly values (December–March). We also calculated for each breeding period the mean value of Sea Surface Temperature (SST), Chlorophyll-*a* Concentration (CHL) and Net Primary Productivity (NPP) from the area within the movement range of tracked breeders (see section S1 in Supplementary Appendix). Since those mean values were highly correlated with NAOw, we only considered the latter for further, as it is an integrated regional index representative of annual environmental conditions. We scaled NAOw to ease interpretability of models.

3.2.5. Space use and behaviour

We processed GPS data using custom-built functions in R (version 3.2.5, R Development Core Team 2016). We split tracks from GPS loggers in separate trips, considering as one foraging trip the route travelled between nest departure and the subsequent arrival to the nest. Only complete trips were considered for further analyses. For every trip, we calculated the distance covered (in km), maximum distance reached from the colony (in km) and duration (i.e. the number of days at sea). Most shearwaters species perform a dual foraging strategy during chick-rearing. With this strategy, adults alternate recurrent short trips to waters near the colony to get resources to feed the chick with less frequent long trips to distant waters to replenish their own body condition (e.g. Magalhães et al. 2008). Therefore, we labelled every trip as short or long using the k-means clustering algorithm with two centres applied on maximum distance reached. We identified individual behaviour along every trip using the Expected-Maximization binary Clustering algorithm (R package *EMbC*, Garriga et al. 2016a) which uses speed and turning angle to classify each location into four behavioural modes: intensive search, extensive search, relocating and resting (see Garriga et al. 2016b for details). We grouped intensive and extensive search into foraging behaviour for further analysis and, for every trip, we calculated the proportion of time invested in foraging, relocating and resting. An exploratory analysis showed most of foraging occurred over the Catalan and Balearic shelfs, in accordance with a prevalent use of neritic waters of the species (Ramos et al. 2013, Reyes-González et al. 2017). Therefore, we quantified the percentage of foraging carried out in each area (using the bathymetry layer provided by Vion & Menot 2009) and accordingly identified the main foraging areas used in every trip.

We investigated foraging grounds computing the fixed Kernel Density Estimation (KDE) for every trip, taking only the locations previously identified as foraging. We used *kernelUD* function from the R package *adehabitatHR* and the ad-hoc method to choose a reasonable bandwidth (h) while avoiding convergence issues (Calenge 2006). The mean bandwidth value from the ad-hoc method (h = 5.6 km) was then used to recompute all KDEs (Haug et al. 2015). Locations were projected to a

Lambert Azimuthal Equal Area projection centred in the breeding colony prior to KDE computation to ensure area comparability. Estimated 50% KDE volumes were considered to represent the foraging ground of each single trip (K50 hereafter), and their sizes were measured in km^2.

3.2.6. Molecular sexing

We extracted 2.0 ml of blood from the tarsal vein of the breeding adults after each GPS recovery. From the blood sample, 0.5 ml was stored in absolute ethanol to identify the sex of all individuals. Molecular sexing was done following Fridolfsson & Ellegren (1999) and based on the detection of the female-specific CHD1-W locus (diagnostic kit from Durviz, Valencia, Spain).

3.2.7. Stable isotope analyses (SIA) of plasma

In marine ecosystems, the ratio of the isotopes of carbon ($\delta^{13}C$) provides spatial information on latitudinal distribution, inshore vs. offshore habitats and benthic vs. pelagic diets (usually, the lower the value the more pelagic the habitat), and thus $\delta^{13}C$ values can be used to infer the origin of food sources (Hobson et al. 1994, Hobson 1999, Bearhop et al. 2002). Consumers generally exhibit a predictable tissue enrichment of the ratio of the isotopes of nitrogen ($\delta^{15}N$) by 3 to 5‰ at each trophic level (Kelly 2000). Hence, $\delta^{15}N$ values can be used to assess the trophic positions of consumers, since higher values correspond to higher trophic position (Cherel & Hobson 2007, Newsome et al. 2007). We performed SIA of both $\delta^{13}C$ and $\delta^{15}N$ to infer habitat/resource use and especially trophic position during the foraging trips (Ramos & González-Solís 2012). We carried out SIA of blood plasma, since the turnover rate of this tissue is about a week, similar to the average duration of shearwater trips (Ramos & González-Solís 2012). Every blood sample collected at a GPS recovery was stored and plasma fractions were separated and froze for later SIA (see section S2 in Supplementary Appendix for details). To link dietary information with foraging grounds and behaviour, every plasma sample was linked to GPS data corresponding to locations in a 6-day window before each blood collection. To assign a main foraging area to this time window, we quantified the percentage of time invested in foraging within Catalan waters and within Balearic waters, and the proportion of time corresponding to fishing vessel attendance events related to the total time foraging (see below).

3.2.8. Fisheries attendance

We quantified for every trip the amount of interactions with all type of vessels from the Spanish fishing fleet operating in the NWM and equipped with Vessel Monitoring System (VMS). In the European Union waters, fishing vessels over 12 m length are fitted with tracking devices constituting the VMS that transmits the boat position with a maximum interval of 2 h (European Commission 2009). We considered that a fishing vessel attendance event occurred when a GPS bird location identified as foraging was within 5 km and ± 1 h from a vessel location and the bird trajectory stayed within ± 30º from the bearing of the vessel (see Soriano-Redondo et al. 2016 for further details).

3.2.9. Statistical analyses

We performed the statistical data analyses using R (version 3.2.5, R Development Core Team 2016). We evaluated sexual differences in (1) space use and behavioural patterns, (2) SIA and (3) fisheries attendance using regression modelling and permutation tests. We used Linear (LMM) or Generalized Linear Mixed Models (GLMM) as appropriate for each model (Harrison et al. 2018). We ensured the selection of the residual family that best fitted the data and avoided overdispersion, using functions provided by the R package *DHARMa* (Hartig 2018). To test the significant effect of predictors in response variables, we used restricted maximum likelihood and likelihood ratio test for LMM and GLMM respectively. When the interactions included in the models were not significant, we ran again the models excluding them for parsimony. We used functions provided by R packages *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017) and *sjPlot* (Lüdecke 2019). We set significance level to 0.05 for all statistical tests.

(1) Sexual differences in space use and behavioural patterns

We built different models including as response variable the maximum distance, the distance covered, the trip duration, the probability of performing long trips and the amount of time invested in each behavioural mode. We included sex, NAOw and the two-way interaction as predictors to test whether environmental variability differently affects individual performance according to sex, and bird identity as random factor. Maximum and total distance were log-transformed prior to modelling with LMM. We used logistic binomial regression to model the probability of performing short or long trips and negative binomial GLMM to model trip duration. We also used negative binomial GLMM to model amount of time invested in each behavioural mode, including the log of the number of locations of each trip as offset to account for different trip duration (Bates et al. 2015). To analyse sexual differences in the size of foraging grounds we performed permutation tests in three different approaches. First, for each year we performed an upper-tailed permutation test to evaluate whether the median value of the observed differences between K50 size of females respect to K50 size of males were larger than expected by chance (Manly 2007). We computed p-values as the proportion of times that the differences of the medians in the permutation distribution were greater than the observed difference in the medians (Manly 2007). Secondly, we also performed a population approach to look for differences in the size of the area occupied by the foraging grounds of each sex at population level (i.e. joint foraging grounds by sex). To get a more representative estimation of the joint foraging grounds, we created 1000 "pseudo-observed" random samples taking 30 K50 from each year and sex. Next, we joined the selected K50 of each sample into single multipolygon objects (*st_union* function from the R package *sf*; Pebesma 2018) and calculated their sizes. Over the random samples of each year we ran an upper-tailed permutation test in the same way as before. We used *twoSamplePermutationTestLocation* function from the R package *EnvStats* (Millard 2013). Lastly, we also addressed the annual expanding/shrinkage of the joint foraging grounds for each sex. If environmental conditions had no influence, we would expect no differences between the sizes of the joint foraging grounds among years with contrasting NAOw. Thus, we generated for each sex a set of null expectations by selecting 1000 random samples in the same way as before but taking K50 from the four years pooled together. The p-values were determined here as the proportion of null expectations that were greater (i.e. expanding, in the case of years with positive NAOw) or smaller (i.e. shrinkage, in the case of years with negative NAOw) than the mean value of the sizes of pseudo-observed samples (Breed et al. 2006, Clay et al. 2016).

(2) Sexual differences in SIA

We modelled δ^{13}C and δ^{15}N values using LMM, considering as predictors sex, NAOw, main foraging area and the time birds were foraging associated with fishing vessels within the 6-day window of plasma. We did not include interaction terms as we did not expect predictors to differently affect physiology of each sex and thus isotopic values. Bird identity was included as random effect. Finally, we compared isotopic niche width and position of birds among years and between sexes. In order to do that, we represented the individual isotopic values of each year in the bidimensional space generated by the isotopic values of $\delta^{13}C$ and $\delta^{15}N$. From that, we calculated mean and covariance matrices for each year and sex to calculate the standard ellipse area (SEA) of each. SEA is a measure of dispersal and can act as a proxy for isotopic niche width (INW hereafter). We performed the analyses using the R package *SIBER* (Jackson et al. 2011) which produces a Bayesian estimation of the SEA (SEAb). This allowed us to compare the probability of a sex's ellipse to be smaller than the other for each studied year (Stable Isotope Bayesian Ellipses in R – SIBER; Jackson et al. 2011).

(3) Sexual differences in fisheries attendance

We estimated the incidence rate ratio as the amount of fishing vessel attendance events related to the amount of foraging during a trip. We used negative binomial GLMM including sex, NAOw and the main foraging area as predictors. Main foraging area was included since the size of fishing fleets operating in each area is different, and so it is the expected probability of fishing vessel attendance. We also included the three-way interaction as the three variables might interplay in the probability of fisheries attendance. Bird identity was included as random factor, and the log of the number of foraging locations was included as offset in the model (Bates et al. 2015).

3.3. Results

We recorded a total of 373 trips from males and 262 trips from females (Table 1). NAOw presented contrasting values over the four years. NAOw values in 2012, 2014 and 2015 were positive (1.04, 1.60 and 1.89, respectively) likely corresponding to unfavourable environmental conditions. In 2013, NAOw reached the lowest negative value (-1.20), likely corresponding to favourable conditions (see Table 1).

Shearwaters consistently used two main foraging areas over the four years: the waters surrounding the Balearic archipelago, especially the Menorca channel, and the Catalan waters (Fig.1). Trips reaching one of these two areas clearly defined a bimodal distribution in maximum distance (see section S3 in Supplementary Appendix). Environmental variability influenced foraging strategies and behaviour, as increasing values of NAOw (i.e. ranging from favourable to unfavourable environmental conditions) positively correlated with an increase in the distance and duration of trips irrespective of the sex, with a greater probability of performing long trips towards Catalan waters and also with the amount of foraging and relocating (Table 2, Fig. 2). Both sexes showed similar time allocation for the different behavioural modes. There was no interaction between sex and NAOw in any model. On average, δ^{13}C values in plasma were higher and δ^{15}N values were lower in shearwaters foraging on Balearic waters than those foraging in Catalan waters (Table 2, Fig. 3B).

We found females to perform on average longer trips, both in distance travelled (males: 65.0 km; females: 83.9 km) and time (males: 1.4 days; females: 1.9 days) (Table 1, Fig. 2A), whereas differences in maximum distance reached was marginally significant (Table 3). Also, the probability of performing long trips towards Catalan waters was twice as high for females as for males (Table 2, Fig. 2B).

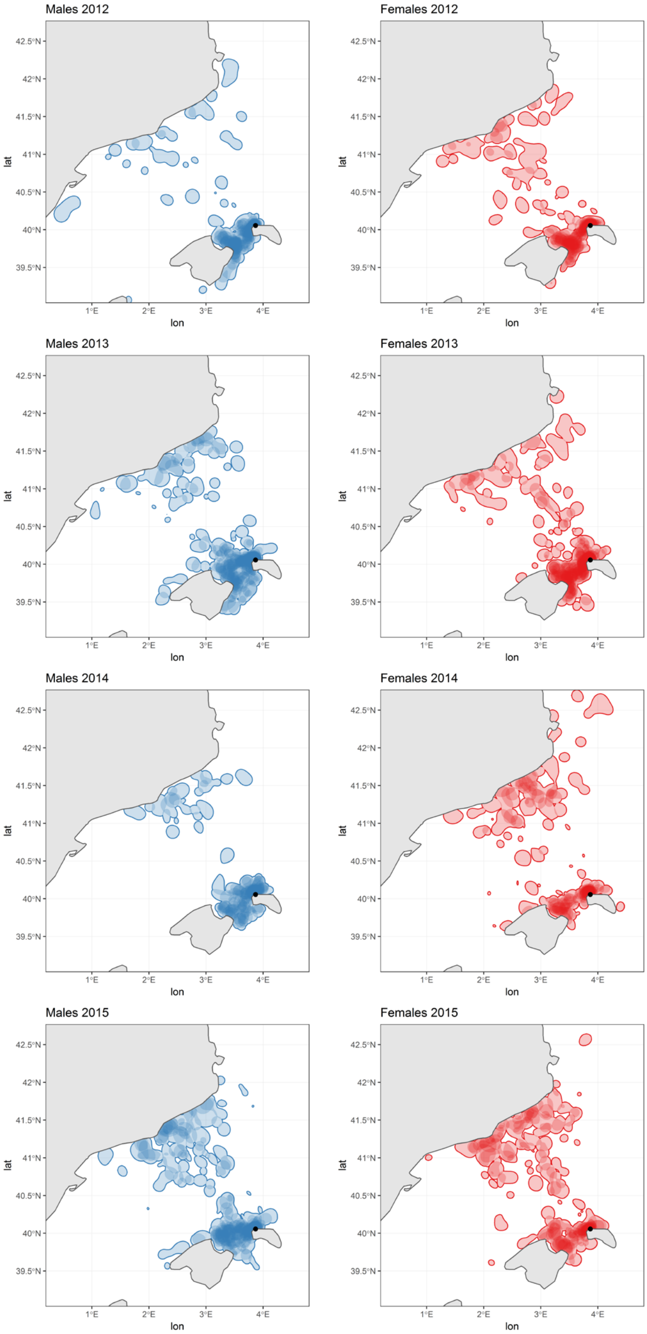

Fig. 1. Annual foraging grounds of males and females of Scopoli's shearwater breeding in Menorca during the chick-rearing period, for four consecutive years. The black circle represents the colony, located in Cala Morell (Menorca, Balearic archipelago). In each box, the solid contour represents the total joint foraging grounds of males (blue) and females (red). Single-trip 50% kernel density contours are showed with transparency to emphasize spatial spreading and overlap between them every year. Two main foraging areas were used to forage, namely Balearic and Catalan waters.

Table 2. **Summary of Linear (LMM) and Generalized Linear Mixed Models (GLMM).** We performed several models to test for the effect of the predictors sex, NAOw, main foraging area and time attending fishing vessels on response variables related to space use, behaviour and isotopic values of Scopoli's shearwaters breeding in Cala Morell, Menorca. LMM = Linear mixed model; GLMM = Generalized linear mixed models; LMMlogT = LMM with response variable log transformed; nbGLMM = Negative binomial GLMM; LogitGLMM = Logistic binomial regression. CAT = Catalan waters. Please note that estimates correspond to odds ratios in the case of LogitGLMM and to incidence rate ratios in the case of nbGLMM. Intercept corresponds to females in Balearic waters. Statistically significant results are highlighted in bold. Also note that in nbGLMM and LogitGLMM, 95% confidence interval not crossing 1 indicates statistical significance.

Model type	Response variable	Fixed effect	Estimate	95% confidence interval	Statistic (*t* | *z*)	*p*
LMM logT	Maximum distance (km)	Intercept	55.8	47.7 – 65.3	50.3	**<0.001**
		Males	0.8	0.7 – 1.0	-1.9	0.062
		NAOw	1.1	1.0 – 1.2	2.5	**0.014**
LMM logT	Distance covered (km)	Intercept	244.6	212.5 – 281.7	76.5	**<0.001**
		Males	0.8	0.6 – 0.9	-2.9	**0.006**
		NAOw	1.1	1.0 – 1.2	3.3	**0.001**
nbGLMM	Trip duration (days)	Intercept	1.8	1.6 – 2.1	8.9	**<0.001**
		Males	0.7	0.6 – 0.9	-3.7	**<0.001**
		NAOw	1.1	1.0 – 1.1	1.7	0.085
LogitGLMM	Probability of long trip	Intercept	0.2	0.1 – 0.3	-6.5	**<0.001**
		Males	0. 5	0.2 – 0.8	-2.6	**0.010**
		NAOw	1.4	1.1 – 1.7	2.7	**0.007**
nbGLMM	% of foraging per trip	Intercept	0.4	0.4 – 0.4	-50.0	**<0.001**
		Males	1.0	0.9 – 1.0	-0.5	0.653
		NAOw	1.0	1.0 – 1.0	-2.0	**0.041**
nbGLMM	% of relocating per trip	Intercept	0.2	0.2 – 0.2	-45.2	**<0.001**
		Males	1.0	1.0 – 1.1	0.7	0.518
		NAOw	1.0	1.0 – 1.1	2.4	**0.018**
nbGLMM	% of resting per trip	Intercept	0.4	0.4 – 0.4	-36.9	**<0.001**
		Males	1.0	0.9 – 1.1	-0.3	0.762
		NAOw	1.0	1.0 – 1.0	-0.3	0.774

Table 2. Continuation.

Model type	Response variable	Fixed effect	Estimate	95% confidence interval	Statistic (t | z)	p
nbGLMM	Fishing vessel attendance	Intercept	0.0	0.0 – 0.0	-28.4	**<0.001**
		Males	1.9	1.1 – 3.4	2.3	**0.024**
		NAOw	0. 8	0.6 – 1.0	-2.4	**0.017**
		Main foraging area – CAT	5.0	2.8 – 9.2	5.3	**<0.001**
LMM	$\delta^{13}C$	Intercept	-18.3	-18.3 – -18.2	-391.9	**<0.001**
		Males	-0.0	-0.1 – 0.1	-0.3	0.733
		NAOw	-0.0	-0.1 – 0.0	-0.9	0.367
		Main foraging area - CAT	-0.1	-0.3 – -0.0	-2.1	**0.040**
		Fisheries attendance time	-0.0	-0.0 – 0.0	-0.4	0.670
LMM	$\delta^{15}N$	Intercept	9.3	9.2 – 9.5	97.7	**<0.001**
		Males	0.4	0.2 – 0.6	3.8	**<0.001**
		NAOw	-0.1	-0.2 – -0.0	-2.1	**0.037**
		Main foraging area – CAT	0.4	0.1 – 0.6	2.8	**0.007**
		Fisheries attendance time	0.1	0.0 – 0.1	2.2	**0.032**

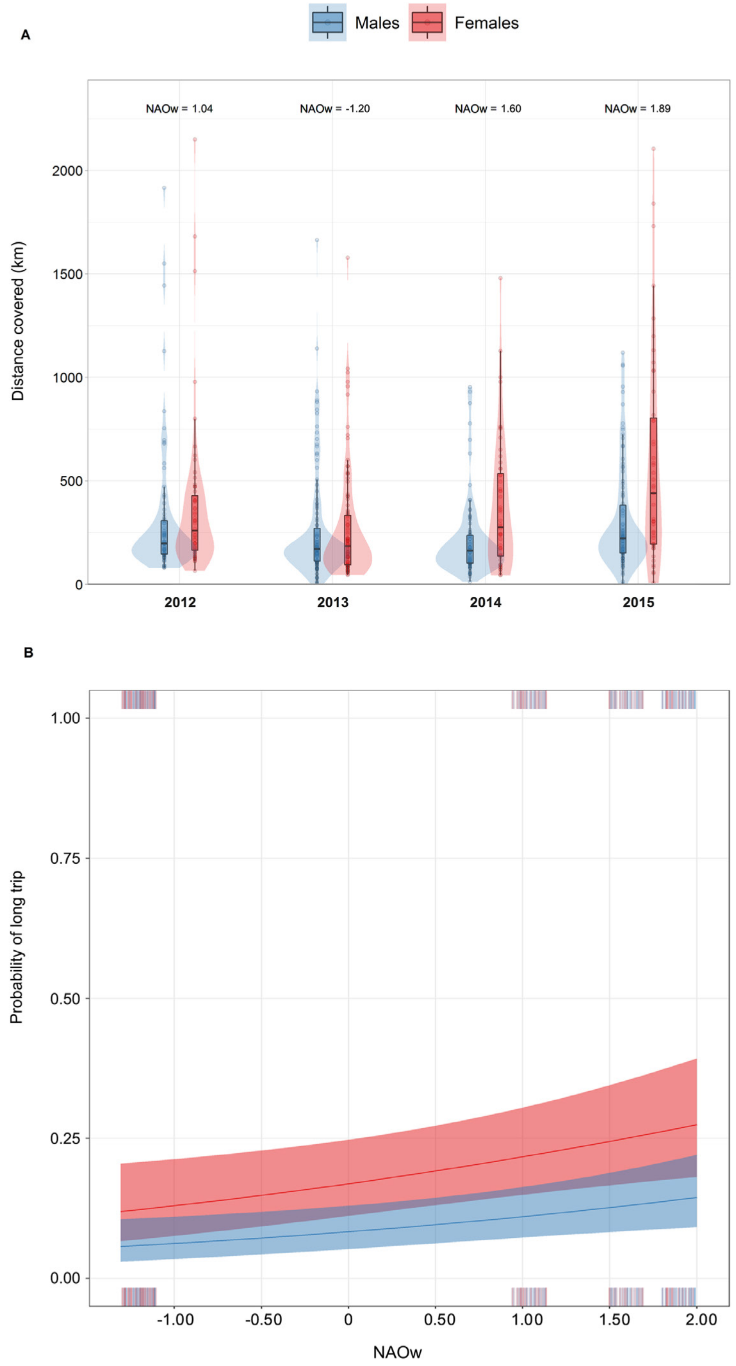

Fig. 2. (A) Observed values of distance covered grouped by sex and year. Each dot represents a single trip. NAOw values for each year are indicated at the top. (B) Predicted probability of performing trips towards Catalan waters from binomial logistic GLMM. Some jittering was applied in rugs of x axis to ease visualization of all cases. Probability was always higher for females and increased with higher values of NAOw.

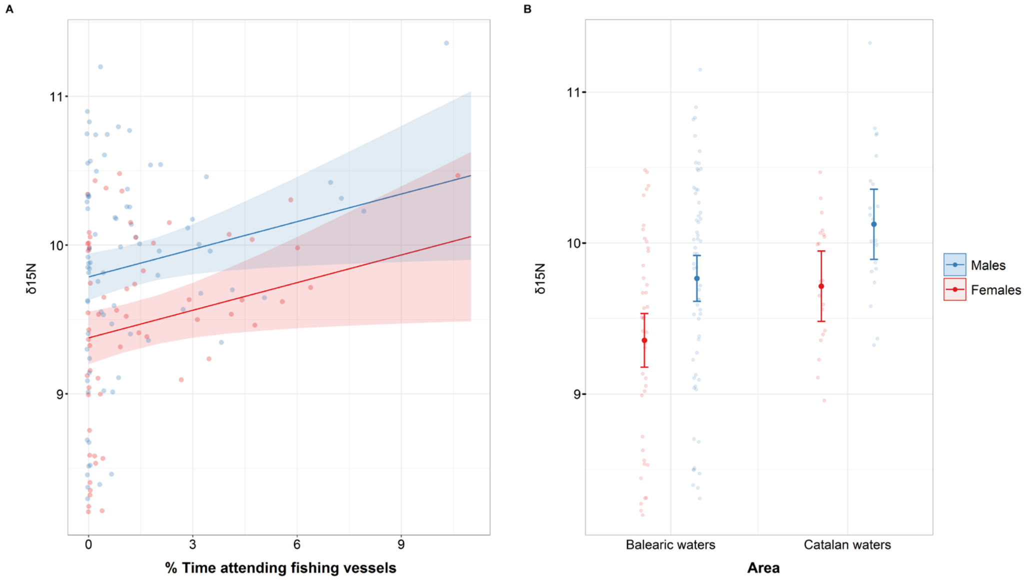

Fig. 3. (A) Marginal estimates of $\delta^{15}N$ values in relation to time attending fishing vessels. (B) 95% confidence interval of marginal estimates of $\delta^{15}N$ values in relation to the main foraging area used by birds within the 6-day window of plasma. Dots represent raw data. Some jittering was applied on raw data in (B) to ease visualization.

Females had significantly greater individual foraging grounds than males in 2014 and 2015, both with positive NAOw (mean values, 2014: 454 km^2 males, 717 km^2 females, $p = 0.017$; 2015: 641 km^2 males, 971 km^2 females, $p < 0.001$; Table 1). Foraging grounds of females at population level were also significantly greater than those of males in the three years with positive NAOw (mean values, 2012: 6194 km^2 males, 8750 km^2 females, $p < 0.001$; 2014: 6159 km^2 males, 11703 km^2 females, $p = 0.017$; 2015: 9814 km^2 males, 14956 km^2 females, $p < 0.001$; Fig. 4A). Moreover, foraging grounds of females at population level significantly shrank in 2013 (likely the most favourable year) and significantly expanded in 2015 (likely the most unfavourable year), whereas those of males did not differ significantly from the null expectation in any year (Fig. 4B).

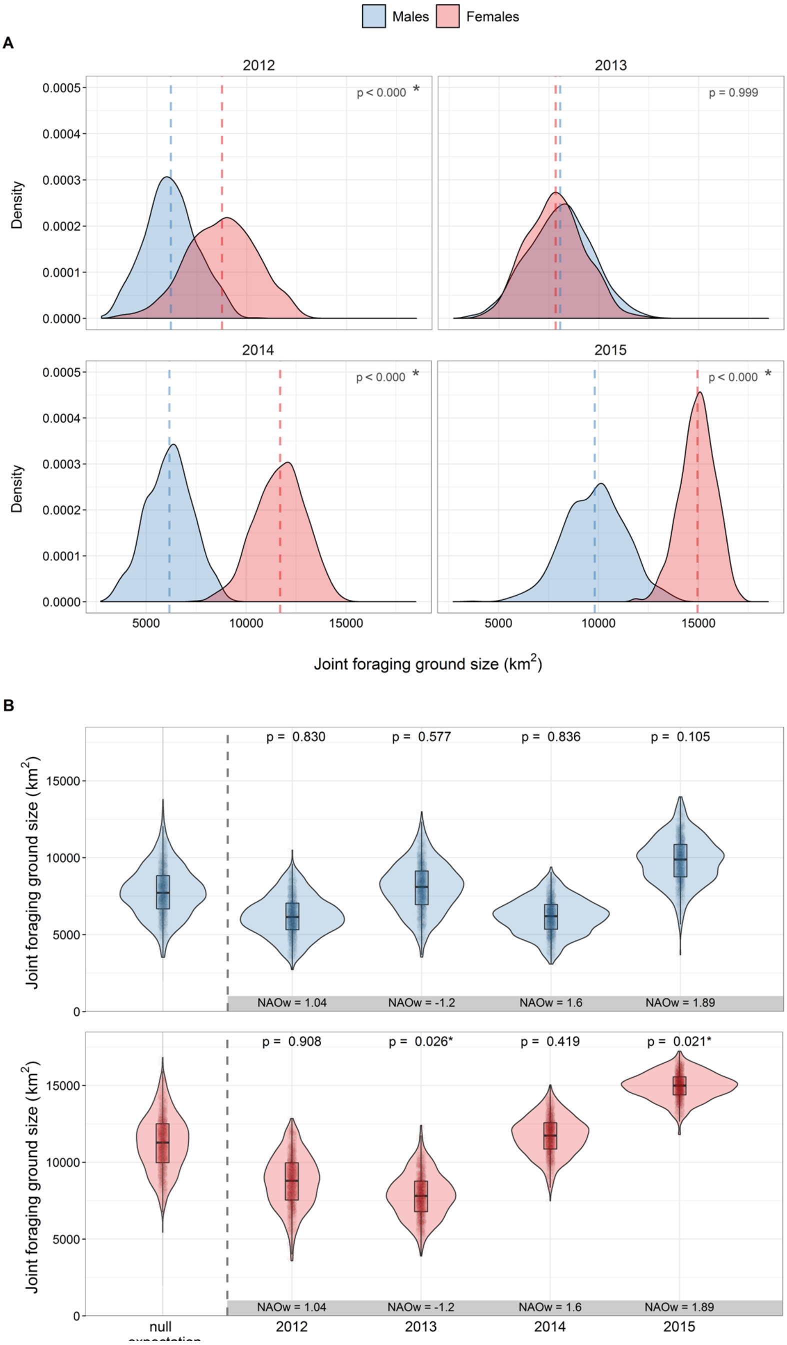

Fig. 4. (A) Sexual differences in the joint foraging ground size every year. For each year and sex, we calculated 1000 "pseudo-observed" joined foraging grounds by selecting 30 trips in each randomly. Dashed lines represent the median values. Significance (p-values) of the upper-tailed permutation tests are shown. (B) We used a similar procedure selecting randomly from pooled data for the four years to build up 1000 null expectations for each sex. We calculated p-values to determine differences respect to null expectations as the proportion of them that were greater or smaller than the mean of pseudo-observed samples.

δ^{13}C values, that allows for discerning the origin of resources (in/offshore and benthic/pelagic) did not differ between sexes. Values of δ^{15}N were consistently higher in males than females across the years (0.4 unities higher on average), suggesting that males were feeding on higher tropic levels than females (Table 3). Percentage of time foraging while attending fishing vessels, despite being always relatively low (up to 15% within 6-day plasma window), correlated significantly with an increase in δ^{15}N values for both sexes. LMM also indicated δ^{15}N values negatively correlated with NAOw (Table 2). Furthermore, males showed a broader INW compared with females, and the overlap of the SEA representing the isotopic niche of males and females was higher in years with negative NAOw (Table 3, Fig. 5).

Table 3. Sexual differences in trophic ecology. Regional environmental conditions, sample size, observed annual means of stable isotopes values (± Standard Deviation, SD) and related metrics from males and females of Scopoli's shearwaters sampled at Cala Morell between 2012 and 2015. NAOw represents the averaged winter (December–March) North Atlantic Oscillation scaled index. SEAb – Bayesian estimates of the standard ellipse areas ± 95% confidence intervals – are used as a proxy of the isotopic niche width of birds (Jackson et al. 2011). Values are mean ± SD. BAL = Balearic waters, CAT = Catalan waters.

		2012		2013		2014		2015	
NAOw		1.04		-1.20		1.60		1.89	
Sex		Males	Females	Males	Females	Males	Females	Males	Females
Individuals (n)		23	16	12	10	12	9	16	9
δ^{13}C		-18.2 ± 0.3	-18.2 ± 0.2	-18.3 ± 0.4	-18.3 ± 0.4	-18.5 ± 0.2	-18.6 ± 0.2	-18.4 ± 0.3	-18.4 ± 0.3
	CAT	-18.3 ± 0.2	-18.3 ± 0.1	-18.4 ± 0.3	-18.3 ± 0.3	-18.5 ± 0.2	-18.6 ± 0.2	-18.5 ± 0.3	-18.4 ± 0.3
	BAL	-18.1 ± 0.3	-18.1 ± 0.1	-18.3 ± 0.4	-18.3 ± 0.4	-18.4 ± 0.2	-18.4 ± 0.0	-18.3 ± 0.4	-18.3 ± 0.0
δ^{15}N		9.2 ± 0.7	8.8 ± 0.6	10.1 ± 0.4	9.9 ± 0.5	9.9 ± 0.5	9.4 ± 0.3	10.3 ± 0.5	9.9 ± 0.3
	CAT	9.9 ± 0.5	9.5 ± 0.4	10.1 ± 0.3	9.9 ± 0.4	10.0 ± 0.6	9.5 ± 0.2	10.4 ± 0.5	9.9 ± 0.3
	BAL	8.9 ± 0.5	8.5 ± 0.3	10.1 ± 0.5	9.8 ± 0.5	9.9 ± 0.5	9.0 ± 0.0	10.2 ± 0.6	10.0 ± 0.0
SEAb		0.4	0.3	0.4	0.4	0.3	0.2	0.4	0.2
		(0.3-0.6)	(0.2 -0.4)	(0.3-0.7)	(0.3-0.6)	(0.2-0.5)	(0.1-0.3)	(0.3-0.7)	(0.1-0.4)

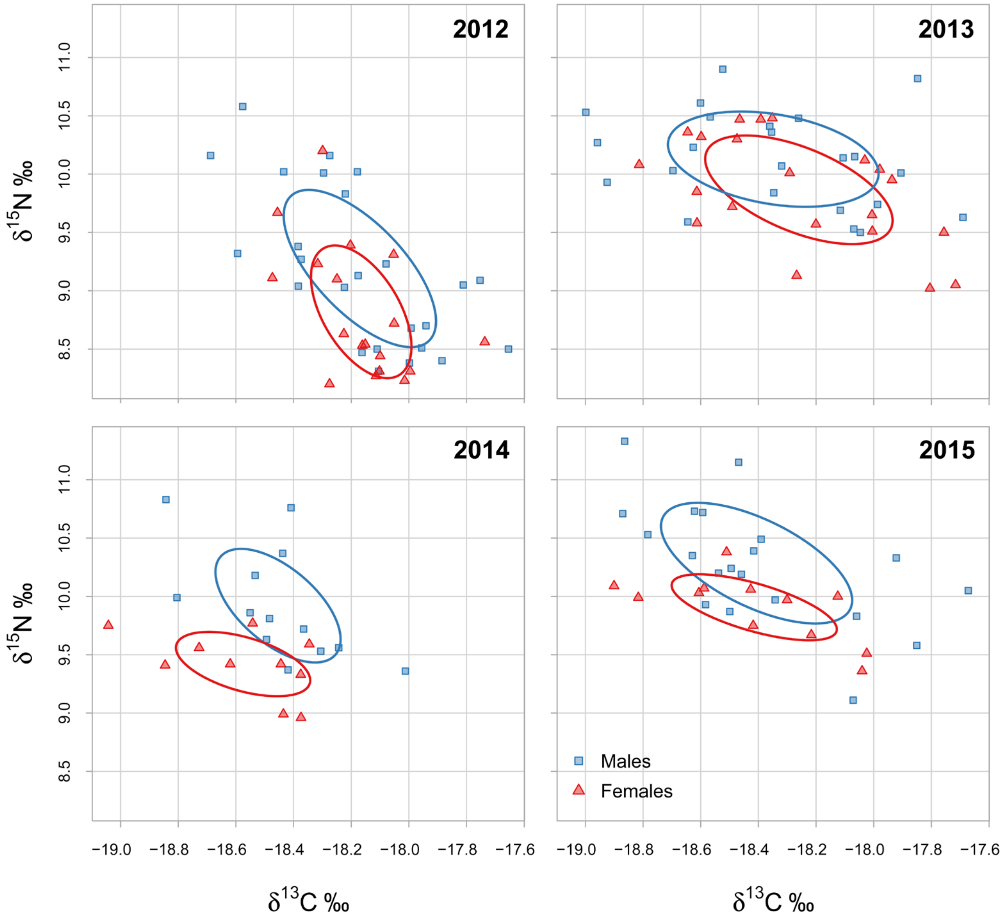

Fig. 5. Isotopic standard ellipse areas, representative of isotopic niche width, for males (blue squares) and females (red triangles) showed by year in the isotopic space of $\delta^{13}C$ and $\delta^{15}N$ values.

We found different incidence rate ratio of fishing vessel attendance, being almost twice as high in males as in females. Moreover, the incidence rate ratio was 5 times higher in Catalan than in Balearic waters, and higher values of NAOw (that is, likely unfavourable environmental conditions) decreased fishing vessel attendance (Table 2). There was no significant interaction between any of the predictors in the model.

3.4. Discussion

We studied sexual differences in foraging movements, resources use and fishing vessel attendance in Scopoli's shearwaters over four years with contrasting environmental conditions by combining tracking, environmental, SIA and VMS information. Despite the slight Sexual Size Dimorphism (SSD) of the species, we found consistent differences in foraging movements, space and resource use and fishing vessel attendance between males and females, indicating a robust segregation in their trophic ecology. Females seem to be outcompeted by males and forced to increase their foraging effort, in particular under unfavourable conditions. Males interacted with fishing vessels to a greater extent, taking more profit of discards and probably exposing them to a higher bycatch risk, than females.

Shearwaters perform a dual foraging strategy

Scopoli's shearwaters consistently used two main foraging areas of the North-Western Mediterranean (NWM) over the four years: the Menorca channel near the colony (short trips) and the Catalan waters (long trips). As commonly found in many procelariiformes, including the closely related Cory's sheawater (Magalhães et al. 2008, Phillips et al. 2017), we found in both sexes a bimodal pattern in trip duration during the chick-rearing period. This is consistent with the dual foraging strategy (Magalhães et al. 2008), with birds performing mostly short trips (~1-day) to the Menorca channel and some longer trips (>3 days) towards Catalan waters. In the dual foraging strategy, short trips are thought to aim at chick-provisioning and long trips are thought to aim at replenishing adult body reserves (Magalhães et al. 2008).

In general, changes in foraging movements, resources use and fisheries attendance were influenced by the conditions of the year. Shearwaters increased foraging effort in years with unfavourable conditions (i.e. positive values of NAOw) and decreased it in favourable years (i.e. with negative values of NAOw). In unfavourable conditions, time allocated to relocating and foraging and the number of long trips increased in both sexes, indicating that shearwaters try to compensate unfavourable environmental conditions by increasing foraging effort. Unfavourable environmental conditions can likely lead to the empoverishment of resource patches, hence forcing both sexes to expend more time searching for food (Hunt et al. 1999). We found both higher fishing vessel attendance and larger use of discards in both sexes during favorable conditions compared with unfavourable ones, possibly because fishing activity, and therefore discards, also increased in favourable years. Government fishery statistics reported the greatest number of trawlers operating and the highest amount of their corresponding landings in 2013 (see section S4 in Supplementary Appendix). Moreover, previous studies have found a positive correlation between landing rates and discards in NWM (Louzao et al. 2011). It is therefore likely that a greater rate of discards led to greatest amount of fishery attendance by shearwaters in the most favourable year within our studied period. This may also explain why shearwaters expanded their trophic niche width with favourable conditions, as indicated by an increase in Isotopic Niche Width (INW) values. Scavenging on discards typically results in greater δ^{15}N values as well as a higher INW due to the consumption of diverse array of demersal and inshore benthonic species with higher and disparate δ^{15}N values (Votier et al. 2010). Therefore, its consumption can lead to an apparent increase in niche width. Conversely, in unfavourable environmental conditions, when more common prey and fishery discards may be scarce, Scopoli's shearwaters in NWM could feed on alternative species, as reported in other populations and conspecific shearwaters (see section S5 in Supplementary Appendix) (Connan et al. 2007, Raymond et al. 2010, Neves et al. 2012, Grémillet et al. 2014).

Sexual segregation exists in fisihing vessel attendance and under unfavourable conditions

We found relevant differences in the foraging ecology of males and females. In agreement with previous studies (Soriano-Redondo et al. 2016), we found Scopoli's shearwaters to interact with fishing vessels operating in both, Catalan and Balearic waters. The sexual differences observed may mostly emerge from differential fishing vessel attendance and consumption of fishery discards between males and females. Males showed a lower foraging effort (shorter foraging distances and time), consistently fed on prey with higher δ^{15}N values, and showed higher INW over the four years when compared to females, indicating relevant differences in diet (Cherel & Hobson 2005) that likely are due to prevalence of males in exploiting fishing vessels as foraging resource. Indeed, fisheries attendance was twice higher in males than in females, which is in line with the male-biased bycatch rate reported for the species in the NWM (Cortés et al. 2018). As mentioned above, feeding on discards typically results in greater δ^{15}N values. Actually, we found an increase of δ^{15}N values with fishing vessel attendance, overall indicating males make a greater use of discards than females. These results suggest males could be outcompeting females from exploiting discards, as previously suggested in other studies (Collet et al. 2015, Cianchetti-Benedetti et al. 2018).

Competitive exclusion may increase with increasing levels of competition. In unfavourable conditions, resource partitioning between males and females increased, as indicated by a decrease in standard ellipse areas (SEA) overlap. In these years, females showed a greater probability of performing long trips towards Catalan waters and expanded the size of their foraging grounds in a greater extent than males. In the NWM, distance between the breeding colonies and the most productive areas located in the Catalan shelf are relatively close for a gliding seabird species (~200km), making the expansion of the foraging areas reasonably feasible. In addition, during the chick-rearing period, the need to frequently feed the chick compels parents to forage near the colony, increasing the spatial overlap of foraging grounds, which can result in local depletion of prey and may increase competition at population level (Lewis et al. 2001). Thus, unfavourable environmental conditions and a greater competence for resources close to the breeding grounds probably increase the preassure to subordinate individuals, especially females, to travel to more distant foraging areas (Hunt & Schneider 1987, Stewart et al. 2000, Paiva et al. 2010). Moreover, unfavourable years seem to be accompanied by a lower activity of fishing fleets in the study area, which probably implies a lower amounts of discards and therefore an increasing competence for them. On the contrary, higher discard rates in favourable years may reduce competitive exclusion behind vessels, allowing more females to access to fishery discards. Indeed, in the most favourable year (2013), females not only increased their INW but also the overlap of their SEA with that of the males (Fig. 5), possibly because females increased discard consuption to similar levels of males.

We found that about 25% of the foraging trips involved interactions with fishing vessels. Despite this rate of fishing vessel attendance may seem low, it should be remarked that the risk of bycatch in any attendance event is high in the association with long-liners (Croxall et al. 2013). Nonetheless, it is known that the risk of bycatch in the NWM differs considerably depending on the longlining fleet métier (García-Barcelona et al. 2010, Báez et al. 2014). Scopoli's shearwaters suffer the highest rate of bycatch among seabirds in the NWM (Valeiras & Camiñas 2003, Cortés et al. 2017) and bycatch rates are considered to be the major cause of mortality at sea pushing adult survival to unsustainable levels (Genovart et al. 2018). In addition, bycatch of the species in NWM is known to be male-biased (Cortés et al. 2018). In accordance with our results, the reported bias towards males in fisheries attendance must be considered for the effectiveness of conservation measures, since a sexual imbalance in mortality at the population level could severely worsen population fecundity, viability and dynamics (Durell et al. 2001, Mills & Ryan 2005, Phillips et al. 2005).

Overall, we demonstrate the existence of robust sexual differences in foraging strategies, foraging areas, resource use and fishing vessel attendance, suggesting males outcompete females from their main areas and resources to a certain extent, particularly under unfavourable conditions. Our results highlight the importance of multi-year approaches to ascertain sexual segregation, particularly in species with slight SSD, since this may pass unnoticed in years with fauvorable environmental conditions. Even in species with slight SSD, sexual segregation in foraging strategies can emerge and lead to different exposure to important threats, thus having important implications for conservation. This study shows human activities can unbalance the risk exposure of males and females, an impact often neglected but that can reduce effective population size and compromise population viability of long-lived species.

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Supplementary Appendix (at the end of the thesis)

S1. Environmental variables

Figure S1. Correlation coefficients between environmental variables (mean of sea surface temperature (sst), mean of sea surface temperature Anomaly (sstA), mean of chlorophyll *a* concentration (chl), mean of net primary production (npp) and the extended annual winter NAO (NAOw) within the movement range of tracked birds.

S2. Stable isotope analysis (SIA) of plasma samples

Table S1. Accepted and mean measured (± SD) of the standard material used in the stable isotope analysis performed in this study, as well as the mean, minimum (Min) and maximum (Max) values obtained. The "n" refers to the number of samples of standards materials used.

S3. Space use by sex and year

Figure S2. Trajectories recorded with GPS loggers showed by sex and year. The black circle represents the colony. Density plots in the right-side point out the bimodal strategy of birds, performing short trips to waters nearby the colony and long trips towards Catalan waters. The number of long trips, however, varied annually, especially in females, likely due to inter-annual variability in the environmental conditions.

S4. Fisheries

Figure S3. Trawling landing (in Tonnes) and number of trawlers operating in Catalan waters (2010 to 2018). Original plot downloaded from http://agricultura.gencat.cat. Years included in this study (2012-2015) are shown in blue. Previous studies have found a positive correlation between landing rates and the amount of discards in the North-Western Mediterranean (Louzao et al. 2011).

S5. Potential prey

Figure S4. Biplot of δ^{15}N-δ^{13}C values of species considered as potential prey (length <15 cm) of Scopoli's shearwaters separated by area (BAL=Balearic waters; CAT=Catalan waters). The shape indicates the corresponding functional group. Error bars represent mean and standard deviation in δ^{13}C and δ^{15}N values of each functional group. Each dot corresponds to a sample from a single species and sampling area. Note that all myctophid species are represented with the same colour. Isotopic values were obtained from Navarro et al. (2009), Valls et al. (2014) and Cardona et al. (2015).

Chapter 4

DOES SEXUAL SEGREGATION OCCUR DURING THE NON-BREEDING PERIOD? A COMPARATIVE ANALYSIS IN SPATIAL AND FEEDING ECOLOGY OF THREE *CALONECTRIS* SHEARWATERS

4

Does sexual segregation occur during the non-breeding period? A comparative analysis in spatial and feeding ecology of three *Calonectris* shearwaters

Abstract

Sexual segregation (SS) is widespread among animal taxa, with males and females segregated in distribution, behaviour or feeding ecology, but, so far, most studies on birds have focused on the breeding period. Outside this period, the relevance of segregation and the potential drivers of its persistence remain elusive, especially in the marine environment, where animals can disperse over vast areas and are not easily observed. We evaluated the degree of SS in spatio-temporal distribution and phenology, at-sea behaviour and feeding ecology during the non-breeding period among three closely related shearwaters: Scopoli's, Cory's and Cape Verde shearwaters (*Calonectris diomedea*, *C. borealis* and *C. edwardsii*, respectively). We tracked 179 birds (92 males and 87 females) from 2008 to 2013 using geolocation-immersion loggers and collected the 13th secondary remige (moulted in winter) for stable isotope analyses as a proxy of trophic level and diet. The global non-breeding distribution did not differ between sexes for the three species, but one specific non-breeding area was visited only by males. Cory's shearwater males remained in areas closer to the colony in a larger proportion compared to females and returned earlier to the colony, probably to defend their nests. Males presented a slightly lower nocturnal flying activity and slightly (but consistently) higher isotopic values of $\delta^{13}C$ and $\delta^{15}N$ compared to females. These differences suggest subtle sexual differences in diet and a slightly higher trophic level in males, but the extent to which sexual dimorphism in bill size can determine them remains unclear. Our study showed that SS in ecological niche in seabirds can persist year-round consistently but at a different extent when comparing the breeding and non-breeding periods. Based on our findings, we propose that SS in these seabird species might have its origin in an ecological specialization derived from the different roles of males and females during reproduction, rather than from social dominance during the non-breeding period.

KEYWORDS

Geolocation · Seabird migration · Stable isotope analyses · Sexual size dimorphism · Non-breeding distribution · Diet specialization

4.1. Introduction

Sexual segregation (SS) is a widespread behavioural and ecological phenomenon in animal taxa (Rubin & Bleich 2005). In many terrestrial and aquatic animal species, males and females differ in their spatio-temporal distribution, at-sea behaviour and feeding ecology (Catry et al. 2005). SS emerges when males and females make different use of some suitable habitats or food resources, which may ultimately result in inter-sexual differences in fitness or survival rates, since sexes may be exposed to different conditions or threats (Harrison et al. 2011, Marra & Holmes 2001). Differences in mortality rate among sexes can lead to an imbalance in the sex ratio, with consequences at the population level and broad implications for population dynamics, species conservation and wildlife management (Durell et al. 2001, Phillips et al. 2005).

Two broad hypotheses have been proposed to explain the general patterns of SS in animals. The social dominance hypothesis suggests that dominant individuals (usually males) tend to exclude subordinates (often females and immatures) from specific areas to access to high quality food resources (Gauthreaux 1978). The ecological specialization hypothesis proposes that habitat segregation arises from sex-specific preferences, tolerance to ecological factors, or specialization in reproductive roles (Selander 1966, Ketterson & Nolan 1983, Morton 1990, Carey et al. 1996). Both hypotheses are not mutually exclusive, and their underlying mechanisms can co-occur and be both cause and consequence (Shine 1989, González-Solís et al. 2000, Catry et al. 2005).

In birds, sexual differences in migration patterns could be explained by mechanisms related to either of these two general hypotheses, such as competition (related to the social dominance hypothesis) or body size and physiology (both related to the ecological specialization hypothesis) (Myers 1981, Gauthreaux 1982, Ketterson & Nolan 1983, Cristol et al. 1999). In general, dominant birds tend to remain sedentary and force subordinate individuals to move to areas further from the breeding grounds to winter (Gauthreaux 1982, Catry et al. 2013, Pérez et al. 2013). Furthermore, individuals with a larger body size and better individual physiology (i.e., better thermal tolerance or fasting endurance), would be able to withstand winter in areas closer to the breeding grounds (Ketterson & Nolan 1976). The tendency of dominant birds to remain resident could also be explained by the arrival time hypothesis, which proposes the earlier arrival of one sex at the end of a migratory journey (related to the ecological specialization hypothesis). According to this hypothesis, the dominant sex tends to be more pressed to arrive earlier at the breeding grounds to gain advantage when competing for better territories or nest sites for breeding (rank advantage hypothesis) (Morbey & Ydenberg 2001) and/or favours more mating opportunities (mate opportunity hypothesis) (Morbey & Ydenberg 2001).

Another indirect mechanism favouring SS is the degree of sexual size dimorphism (SSD) of the species. SSD can contribute to social dominance, as the larger sex is usually the dominant one. Social dominance of one sex can lead to the spatial exclusion of the other at various spatial scales, ranging from subtle differences in microhabitat to disparate geographical distributions (Catry et al. 2005, Staniland 2006). Nevertheless, SSD can also lead to ecological specialization, due to divergent nutritional and energetic requirements (Main & Coblentz 1990, Ruckstuhl & Neuhaus 2002, Newton 2008), and/or to niche or dietary specialization. The latter occurs when males and females use similar foraging areas but specialize on different prey types due to the morphological differentiation in feeding or locomotion structures (Bearhop et al. 2006, Phillips et al. 2011).

Since ecological specialization may arise from differences in the roles of males and females during reproduction, sex-specific differences in spatio-temporal distribution and feeding ecology have been widely studied during the breeding period (Thaxter et al.

2009, Weimerskirch et al. 2009, Elliott et al. 2010, Stauss et al. 2012). However, studying behavioural and ecological sexual differences out of the breeding period, especially among migratory species, can be challenging due to sampling constraints and limited accessibility to individuals, particularly in the marine environment. As a result, the relevance of SS and the mechanisms of its persistence over the non-breeding period remains elusive (see Croxall et al. 2005, Alves et al. 2013, Pérez et al. 2013, Müller et al. 2014).

Our capacity to study the spatial and feeding ecology of migratory species during the non-breeding period has improved considerably in the last decades due to the possibility to combine the deployment of light-level geolocation devices (geolocators hereafter) and stable isotope analysis (SIA). Geolocators can inform us about the year-round phenology, movements, distribution and at-sea activity patterns (in those cases where loggers are also equipped with an immersion sensor) of a given species. SIA can provide us with information on the feeding and spatial ecology when species feed on isotopically different prey or in areas with distinct isotopic baseline values (Ramos & González-Solís 2012). Feathers are metabolically inert after growing and, therefore, their isotopic values reflect the food assimilated by birds during their synthesis (Hobson & Clark 1992, Ramos & González-Solís 2012). Thus, by analysing feathers moulted during the non-breeding period, we can infer the feeding ecology of birds during such an otherwise inaccessible life stage.

Calonectris shearwaters are wide-ranging species, performing long-distance migrations across ocean basins after the breeding period and spreading over diverse non-breeding areas (Thibault et al. 1997, González-Solís et al. 2007), thus exposing the individuals to variable environments that can lead to SS in foraging strategies in different ways (e.g. Bearhop et al. 2006, Phillips et al. 2009, Ceia et al. 2012, Åkesson & Weimerskirch 2014) (Figure 1). These species are relatively well-studied during the breeding period, and many studies have been done with respect to their SS (e.g. Navarro et al. 2009, Ramos et al. 2009a, Ramos et al 2009b, Alonso et al. 2014, Werner et al. 2014, Cianchetti-Benedetti et al. 2017, Matsumoto et al. 2017, Paiva et al. 2017). In these species, SS in foraging behaviour and feeding ecology may be shaped by annual and seasonal prey availability (Paiva et al. 2017), differences in reproduction duties over the breeding period (Ramos et al. 2009b, Werner et al. 2014), and/or could be related to SSD between sexes (Alonso et al. 2014, Cianchetti-Benedetti et al. 2017). However, while many of these studies did find evidence of sexual differences in foraging and feeding ecology during the breeding period (Ramos et al. 2009b, Alonso et al. 2014, Werner et al. 2014, Cianchetti-Benedetti et al. 2017, Matsumoto et al. 2017, Paiva et al. 2017), many others did not find any clear difference (Navarro et al. 2007, Navarro et al. 2009, Ramos et al. 2009a). Nonetheless, the degree to which SS in foraging performance continues out of the breeding period is still poorly known in these species (Müller et al. 2014).

Figure 1. Breeding pair of Cory's shearwaters at Montaña Clara colony (Canary Islands) photographed inside their nest in 2008. Photograph by Jacob González-Solís.

In this study, we evaluated the degree of SS in spatial and feeding ecology during the non-breeding period of three closely related shearwaters: the Scopoli's, Cory's and Cape Verde shearwaters (*Calonectris diomedea, C. borealis* and *C. edwardsii*, respectively). In general, we expect that SS in spatial and feeding ecology occurring during the breeding period will not persist during the non-breeding period, since during this period seabirds do not have different reproductive roles, are not constrained to return to their nests and can range for many thousands of kilometres to winter in the most productive areas of the ocean (Shaffer et al. 2006, Bost et al. 2009, Egevang et al. 2010), reducing between-sex competition and partitioning of food resources (Phillips et al. 2011). Specifically, we aim to test the following three hypotheses: (1) As the larger size of males has been related to a greater involvement in nest defence at the beginning of the breeding period (Hedd et al. 2014, Werner et al. 2014), we expect males to return to the breeding colonies earlier than females, in accordance with the arrival time hypothesis. (2) Since during the non-breeding period foraging ranges are not constrained, and shearwaters disperse over wider areas to winter (Shaffer et al. 2006, González-Solís et al. 2007), we expect that both sexes would share the same non-breeding areas, and males would not exclude females from areas with high quality food resources. (3) Previous studies found differences between sexes in the bill shape and size to be poor predictors of the way males and females (of Cory's shearwaters) exploit the marine environment (Navarro et al. 2009, Ramos et al. 2009b). Moreover, between-sex competition for resources is less intense during the non-breeding period (González-Solís et al. 2000). Thus, we expect that males and females would not present differences in their feeding ecology during this period and would feed on similar prey items. Predictions (2) and (3) would refute the social dominance hypothesis for the non-breeding period, whereas prediction (1) would support the arrival time hypothesis for migratory seabirds. To this end, we evaluated sexual differences during the non-breeding period of Scopoli's, Cory's and Cape Verde shearwaters in: (1) spatio-temporal distribution (inferred through geolocation data), (2) at-sea activity behaviour (inferred through immersion data), and (3) feeding ecology (inferred through SIA on one specific feather known to be moulted in the winter quarters). Finally, as greater SSD can lead to greater SS (Abouheif & Fairbairn 1997, Fairbairn 1997), we also determined the degree of SSD of each species and explored the potential influence of bill size on its feeding ecology.

4.2. Materials and methods

4.2.1. Study species and sampling protocol

Scopoli's shearwater is an endemic breeding species in the Mediterranean Basin, ranging from the Iberian coast to the Adriatic and Aegean Seas (Gómez-Díaz & González-Solís 2007). Cory's shearwaters breed on several islands in the northeast Atlantic Ocean, and in a few small colonies in the western Mediterranean Sea (Gómez-Díaz et al. 2009). The Cape Verde shearwater is an endemic breeding species in the Cape Verde Islands (Hazevoet 1995). Scopoli's and Cory's shearwaters are classified as "Least concern" according to the Red List criteria of the International Union for the Conservation of Nature (IUCN) (BirdLife International 2018), whereas the Cape Verde shearwater is listed as "Near Threatened" due to its restricted breeding distribution (Hazevoet 2003).

Calonectris shearwaters breed mainly on islands and islets, nesting in burrows and crevices. Breeding females lay a single egg per season, and both parents share similar incubation and chick-rearing duties throughout the breeding season (Thibault et al. 1997, Granadeiro et al. 2006). All three species show slight sexual dimorphism in body size, with females being slightly smaller than males in wing length, tarsus length and bill dimensions and having a less robust shape (Massa & Lo Valvo 1986, Granadeiro

1993, Navarro et al. 2009). The breeding phenology of the three species is similar in time: birds return to the colony from the non-breeding areas in late February/early March, the laying period begins in the second half of May and chicks start hatching in mid-July. Fledglings usually leave the colonies from mid-October to early November (Hazevoet 1995, Thibault et al. 1997, Granadeiro 1999). All three species spend the non-breeding period in the Atlantic Ocean, mainly in the South Atlantic in areas associated with major upwellings (such as the Benguela and Angola Currents and the Brazil Current), and the Canary Current. However, Cory's shearwater can present a broader distribution, with some birds wintering in the North Atlantic and in the southwestern Indian Ocean (Petry et al. 2000, González-Solís et al. 2007, Müller et al. 2014).

In up to five breeding colonies (Table 1), adult birds were captured in their burrows during the breeding period, ringed and tagged with geolocators. During the subsequent breeding period, we recaptured the birds, retrieved the geolocator, cut the 13th secondary remige (S13 hereafter) for SIA, and we equipped the birds with a new geolocator. During one of the recaptures, we also took a blood sample for molecular sexing and biometric measurements for SSD assessment.

Table 1. Summary characteristics of the study colonies and the number of males and females of Scopoli's, Cory's and Cape Verde shearwaters sampled and tracked in the study period.

Species	Breeding colony	Longitude (°)	Latitude (°)	Sampling years	Sample size		Tracks	
					Males	Females	Males	Females
Scopoli's shearwater	Pantaleu islet (Balearic Islands)	2.35	39.57	2009 - 2013	22	22	35	35
Cory's shearwater	Vila islet (Azores Islands)	-25.17	36.94	2010 - 2012	12	6	16	9
	Montaña Clara (Canary Islands)	-13.53	29.29	2011 - 2013	9	11	12	16
	Veneguera (Canary Islands)	-15.78	27.84	2008 - 2013	44	38	92	76
Cape Verde shearwater	Curral Velho islet (Cape Verde)	-22.78	15.96	2008 - 2011	5	10	10	14

4.2.2 Molecular sexing

All individuals in the study were molecularly sexed. DNA was extracted from ethanol-preserved whole blood using a Real Pure genomic DNA extraction kit (Durviz, Spain) following the manufacturer's instructions. Polymerase Chain Reactions (PCRs) were performed following the method of Fridolfsson & Ellegren (1999), previously used to identify the sex in a large variety of Procellariiform species. Sex determination was based on the detection of a female-specific locus, CHD1-W.

4.2.3 Biometric measurements and sexual size dimorphism (SSD)

We measured five biometric variables on 44, 54 and 16 individuals of Scopoli's, Cory's and Cape Verde shearwaters, respectively: tarsus length, culmen length, maximum head length (head plus bill length), bill depth at the base and bill depth at the nostrils. Measurements were taken using digital callipers (± 0.01 mm). We assessed the SSD for each biometric measurement and for each study species. SSD index (SSI hereafter) was calculated as:

$$\text{SSI}=\left(\frac{\textit{male's average} - \textit{female's average}}{(\textit{male's average} + \textit{female's average}) \times 0.5}\right) \times 100 \text{ (Storer, 1966)}$$

This index is recommended due to its simplicity and because it maintains symmetry around a neutral zero, indicating monomorphy. Furthermore, it complies with the convention of positive values in cases where males are the larger sex and negative values in cases where females are the larger ones (Greenwood 2003). To check the influence of bill SSI on the feeding ecology of the shearwaters, we pooled all individuals measured (N=144) and performed a principal component analysis (PCA) on culmen length, maximum head length, bill depth at the base and bill depth at the nostrils per each individual. Axis 1 explained a high proportion (92%) of the total variance (see Table S1 in Supplementary Appendix). Therefore, the first principal component scores (scores on Axis 1, hereafter referred to as PC1 scores) were used as a proxy of bill size in further statistical analyses (Rising & Somers 1989).

4.2.4 Geolocation light data

To evaluate whether adult males and females of each species differ spatially in their distribution and/or phenology during the non-breeding period, we equipped several adult birds of each species with geolocators. The geolocator was attached to a PVC ring with a cable tie, and the ring was put on the leg of the bird. The weight of the geolocators varied from 1.8g to 4.5g, depending on the model (models Mk4, Mk9, Mk13, Mk14, Mk18-H, Mk19 from the British Antarctic Survey and Mk3005 from Biotrack), corresponding to less than 1.2% of bird body mass, which is known to have negligible effects on the birds (Igual et al. 2005, Carey 2009). Overall, we collected information from 70, 221 and 24 geolocators from Scopoli's, Cory's and Cape Verde shearwaters, respectively, deployed on 182 individuals (Table 1).

Geolocators are devices that record and store ambient light information. The intensity of light is measured every 60 seconds and the maximum reading is recorded in 5 or 10-minute intervals, depending on the model. Sunset and sunrise times are estimated from thresholds in light curves and are converted into latitudes and longitudes since every location on the planet has a unique combination of time of sunrise and photoperiod in each hemisphere (Hill 1994), except during the equinoxes. Latitude was derived from day length, and longitude from the time of local midday with respect to Greenwich Mean Time. Thus, we assessed two positions of the bird per day with an average accuracy of approximately 186 ± 114 km (Phillips et al. 2004). Light data was analysed visually for every geolocator, using TransEdit and BirdTracker softwares (British Antarctic Survey, UK) and unrealistic positions were filtered by: (1) removing data during equinoxes due to the inaccuracy of latitude estimation (ca. 20 days before and after the equinoxes); and (2) removing the positions from light curves with obvious interference during the times of sunset or sunrise. We set to 20 the threshold light level considered as the transition between day and night in order to avoid interferences of light during the night and darkness during the day. Before obtaining the trajectory of each bird, sun elevation angles (ranged for -6° to -3°) were calculated based on known positions obtained during a calibration period (approximately one week) carried out before the deployments and after recoveries at the breeding colonies. Finally, we smoothed the filtered data twice by interpolating intermediate fixes between successive locations as recommended by Phillips et al. (2004).

To assign each bird (and year) to a single non-breeding area, we first computed the utilization distribution kernel (KUD hereafter) with previously filtered geolocation data using the function "kernelUD" (R package adehabitat v.1.8.71, Calenge 2006). We used a bandwidth equivalent to 186 km (~2º, depending on latitude) to account for the average reported error in geolocation (Phillips et al. 2004). Later, we extracted the 50% density contour of the KUD and determined the centroid, using the function "gCentroid" from the R package rgeos (Bivand & Rundel 2017). We performed a Chi-square test per colony based on the proportion of each sex in each non-breeding area to determine if a sexual preference for the use of specific non-breeding areas existed. In case the 50% density contour of the KUD of a bird was comprised by more than one polygon, the centroid considered for assigning a main non-breeding area was the one corresponding to the polygon where the bird spent the highest number of days.

In order to determine differences between sexes in the size of the areas used during winter, we first computed KUD using filtered positions for each non-breeding area and year using a Lambert Azimuthal Equal Area projection centred in the centroid of locations to allow area comparability. Next, we calculated the size of the 95% and 50% KUD contours (function "gArea", package rgeos, Bivand & Rundel 2016), which were considered to represent the general use and core areas of the wintering distribution, respectively. Lastly, we quantified the amount of overlap between females and males in the general use and core areas of wintering distribution using the "kerneloverlap" function and "HR" method of the adehabitatHR package (Calenge 2006).

To infer the migratory phenology of our study birds, the filtered positions were inspected visually using Locator software (British Antarctic Survey, UK). Departure dates (from colonies and non-breeding areas) were defined as the first position outside the cluster of positions of the 10 previous days, when birds shifted behaviour and began a rapid directional flight moving away from that cluster. Similarly, arrival dates were defined as the first position of the birds within the cluster of the positions recorded during the days after a rapid directional flight. During the equinoxes the departure and arrival dates were determined based on the birds' longitude changes (not affected by the equinoxes) as, in most cases, the migratory movement was mainly longitudinal (e.g. Scopoli's shearwater departure from the colony westward toward the Atlantic. In the case of arrival at the breeding colonies occurring during the equinox, we defined the arrival date as the first night the bird spent all night dry (resting at the colony).

4.2.5 At-sea activity data

The geolocator models used also incorporate a salt-water switch that measures conductivity from immersion in saltwater every 3 seconds, and combines this information at every 10-minute interval. Given the sampling interval (3 s), the values recorded at the end of each 10-minute period range from 0 (10-minute period in dry mode = no conductivity detected) to 200 (10-minute period in wet mode). This data can be used to infer the behaviour of the birds during the non-breeding season: complete dryness (0) means that the birds are flying; complete wetness (200) means that the birds are resting (sitting on the sea surface) or diving; and alternate modes between dry and wet (1-199) mean that birds are alternating flying and resting, or could also suggest foraging behaviour (Lecomte et al. 2010, Mattern et al. 2015).

To assess if males and females behave differently at sea during the non-breeding period, we calculated the night flight index (NFI; Dias et al. 2012b) of every bird for the period spent in the main non-breeding area. The ratio of nocturnal/diurnal activity may be associated with prey targeted and thus can provide information about feeding strategies (Spear et al. 2007, Regular et al. 2010, Dias et al. 2016). NFI represents the difference between the proportion of time spent flying during darkness and the proportion of time spent flying during daylight, divided by the highest of these two values, and it varies between -1 (flight activity exclusively during daylight) and 1 (flight activity exclusively during darkness). Moonlight intensity affects activity patterns of shearwaters (Yamamoto et al. 2008, Dias et al. 2012a). Thus, to control for the influence of moonlight intensity on NFI values, we selected data for an entire lunar cycle (28 days) within the non-breeding period per individual and year, calculated the NFI for every day of this lunar cycle and, finally, calculated the mean NFI value per individual and year.

4.2.6 Stable isotope analyses (SIA)

SIA of feathers can be used to study the feeding ecology of seabirds (Hobson 1999). Feathers become metabolically (and isotopically) inert once fully formed and maintain the isotopic composition of the period and area when they were synthesized, independently of the sampling time (Hobson & Norris 2008). Knowing the moulting patterns of the study species is crucial for SIA, since it allows us to choose which feather to analyse, depending on the period of interest. The moulting patterns of Scopoli's and Cory's shearwaters are relatively well known (Camphuysen & Van Der Meer 2001, Alonso et al. 2009, Ramos et al. 2009c), and they are rather similar between these species. Thus, we assumed it would also be similar for the Cape Verde shearwater. We collected the S13 remige for SIA as this feather is known to be moulted at the middle to end of the non-breeding period in Scopoli's and Cory's shearwaters (since the moult of secondary remiges is asynchronous, and the foci of 12th to 16th secondary remiges are the last to be moulted; Ramos et al. 2009c). In general, $\delta^{15}N$ increases by 3 to 5‰ with each trophic level (DeNiro & Epstein 1981). $\delta^{13}C$ also increases with trophic level, although in a smaller proportion (approximately 1‰) (Rau et al. 1992). The main causes of variations in $\delta^{13}C$ are differences in photosynthetic biochemistry within and among marine primary producer communities (Farquhar et al. 1989, Robinson 2001). Hence, in marine ecosystems, we can infer the origin of food sources from the $\delta^{13}C$ gradients that exist between water masses, gradients between inshore/offshore waters and benthic/pelagic habitats, while $\delta^{15}N$ values can be used to assess the trophic positions of consumers (Cherel & Hobson 2007, Newsome et al. 2007).

Once at the laboratory, feathers were washed in a 0.25 M NaOH solution, thoroughly rinsed twice in distilled water to remove any surface contamination, and dried in an oven at 40°C to constant mass. Afterwards, we freeze-milled all feathers to fine powder in a cryogenic impact grinder (Freeser/mill Spex Certiprep 6750; Spex) operating at liquid nitrogen temperature. We weighed subsamples of 0.30 to 0.32 mg of feather powder and placed them in tin capsules. These samples were oxidized in a Flash EA1112 and TC/EA coupled to a stable isotope mass spectrometer Delta C through a Conflo III interface (ThermoFinnigan) and, finally, $\delta^{13}C$ and $\delta^{15}N$ values were determined. Isotope ratios (R) of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ are expressed conventionally in δ units as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1],$$

where X (‰) is ^{13}C or ^{15}N and R are the corresponding ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$ related to the standard values. The international standards for SIA are Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N_2 (AIR) for nitrogen. The SIA were performed at the Serveis Científico-Tècnics of the University of Barcelona (Spain), where international standards (IAEA CH_7, IAEA CH_6 and USGS 40 for C and IAEA N_1, IAEA N_2, IAEA NO_3 and USGS 40 for N) are applied and two standard material samples are inserted every 12 feather samples to calibrate the system and compensate for any drift over time (Böhlke & Coplen 1995, Böhlke et al. 2003, Coplen et al. 2006, Qi et al. 2003) (Table S2 in Supplementary Appendix). The overall measurement error is on average of 0.2‰ for carbon isotopes and 0.3‰ for nitrogen isotopes. All the samples were homogenized by milling them to a fine powder, so we believe that was not necessary to run duplicates The entire feather analysis methodology was conducted following the “principle of identical treatment” (Bond & Hobson 2012).

Isotopic data was used to characterize the isotopic niche widths (INW) of each sex through Bayesian statistical ellipses (stable isotope Bayesian ellipses in R – SIBER). We compared INW using a Bayesian estimate of the standard ellipse area (SEAb) to test the probability of a group ellipse of one of the sexes being smaller than the other (Jackson et al. 2011). To have a correct estimation of the ellipses, we only considered those non-breeding areas and years used for a minimum of 4 birds per sex. Despite the small sample size, it is known that the Bayesian implementation of the ellipse area measurement is less affected by sample size than the convex hull, SEA and SEAc (Jackson et al. 2011). In addition, using the Bayesian estimation allowed us to provide uncertainty measures (95% Credible Intervals) around point estimates for the ellipse areas.

4.2.7 Statistical analyses

We performed linear mixed-effects models (LMM) to check for sexual differences in the following spatial, phenological, behavioural and feeding ecological features:

(1) Phenological parameters of the migration (represented as day of the year): departure date from the breeding colony (post-breeding migration), days in transit to the non-breeding areas, total duration of the non-breeding period, days in the non-breeding areas, onset of the pre-breeding migration, days in transit returning to the colony and arrival at the breeding colony. These parameters can only be calculated for migratory birds, so we excluded those birds that remain year-round near the breeding grounds. Nevertheless, we also tested for differences in the date of arrival at the breeding colony between migratory and non-migratory males of Cory's shearwater and between non-migratory males and females of Cory's shearwater;

(2) Maximum distance travelled from the colony to the centroid of the wintering distribution;

(3) Mean size of the core areas of the wintering distribution;

(4) NFI values;

(5) INW estimated for each non-breeding area, as indicated by the SEAb values;

(6) Values of $\delta^{13}C$ and $\delta^{15}N$ assessed on S13 remiges.

Regarding the structure of the models, we always included sex and species as fixed effects. In the models testing for differences in the arrival date at the breeding colony between migratory and non-migratory Cory's shearwater males, we included migratory behaviour (migratory or non-migratory) and non-breeding areas as fixed effects. In the models of $\delta^{13}C$ and $\delta^{15}N$, we also included bill size (PC1 scores of bill measurements) as a covariate when testing the effect of the sexual dimorphism on trophic ecology. In the models considering INW, we also included the size of the core area of the wintering distribution within non-breeding areas as a covariate. Except when modelling INW, bird identity and year were included as random effects to avoid pseudo-replication and non-independent measurements. When modelling INW, we only included non-breeding area as a random term, since the INW is calculated by each sex and it is not an individual estimate. When determining the factors affecting migration phenology and the values of $\delta^{13}C$ and $\delta^{15}N$, we also included non-breeding area as a random term, as well as bird identity and year. Lastly, in the models testing for differences in arrival date at the breeding colony between migratory and non-migratory males of Cory's shearwater, we included the breeding colony as a random term.

All statistical analyses were performed using R software (version 3.2.5, R Development Core Team 2010). LMMs were conducted with the function "lmer" (R package lme4, Bates et al. 2015). To ensure accomplishment of normality and homoscedasticity, we visually inspected Q-Q plots scatter plots of residuals vs fitted values. We created a set of competing models (the first as the full model, including all fixed factors and double interactions) and selected the most parsimonious models, i.e., the models that better explain our data using fewer parameters, based on the Akaike's Information Criterion corrected for small sample sizes (AICc) using the function "dredge" (R package MuMIn, Kamil 2017). According to the AICc weight (Burnham & Anderson 2002), we removed non-significant terms from our models. When ΔAICc

was < 2 between our best models, these models explained the data equally well, thus we could not determine which one was the most parsimonious (Burnham & Anderson 2002). To address this issue, we performed model averaging using the function “model.avg” (R package MuMIn, Kamil 2017) of those models with ΔAICc < 2 to obtain estimates for our variables. Finally, we performed post-hoc comparisons by calculating the differences between the least-squares means within fixed factors of our best models using the function “difflsmeans” (R package lmerTest, Kuznetsova et al. 2015). Whenever multiple comparisons with the same variables were performed, we applied Bonferroni corrections to calculate the correct statistical significance according to the numbers of tests performed.

4.3. Results

4.3.1 Biometric measurements

SSI were generally low. Tarsus of Cory’s shearwater presented the lowest value (3.4%), whereas bill depth at the nostrils in Scopoli’s shearwater showed the highest value (13.4%). Males were, on average, larger than females for the three species, although values of standard deviations overlapped in some extent (i.e. larger females overlapped in size with smaller males). For the three species, differences were more pronounced in bill measurements than in tarsus or maximum head lengths. Scopoli’s shearwaters showed the highest SSI among the study species (Table S3 and Table S4 in Supplementary Appendix).

4.3.2. Spatial ecology

4.3.2.1. Migratory patterns

When testing for sex and species effects on eight migratory parameters, the most parsimonious LMMs always retained species as explanatory factors, and most models also retained sex (Table S5 in Supplementary Appendix). No sexual differences were found in the maximum distance travelled from the colony to the centroids of the non-breeding areas or in the number of days in transit to the non-breeding areas (Table S5 and S6 in Supplementary Appendix). For the rest of variables describing migratory patterns, the two best models explained our data equally well ($\Delta\text{AICc} < 2$) and, thus, we performed model averaging between them. Males left the colonies in autumn 4 days earlier, on average, than females. The total duration of the non-breeding period (from departure and until the return to the breeding colony), as well as the number of days in the main non-breeding areas, was greater for males than for females. Males started the pre-breeding migration approximately 1 day earlier than females, and arrived about 3 days earlier at the breeding grounds, spending fewer days in transit when returning to the colony (Table S5 in Supplementary Appendix).

Since some Cory's shearwater individuals from Vila and Veneguera did not migrate and remained in areas close to their colonies, we tested whether the return date to the colony differed between non-migratory and migratory birds. Most parsimonious LMM retained the migratory behaviour, but did not retain non-breeding areas as an explanatory factor. Non-migratory males arrived about 23 days earlier at the breeding colonies when compared to migratory males. The random effect bird identity explained a higher proportion of the variance not explained by fixed factors than did year or breeding colony factors (Table 2).

Table 2. Linear mixed models (LMMs) testing for potential effects of migratory behaviour and non-breeding area on the arrival date at the breeding colony of male Cory's shearwaters. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; $AICc_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model is shown in bold. (b) Mean estimates (and 95% confidence intervals in parenthesis) of the fixed effects. (c) Variance (± SD) and random variance explained (calculated as the percentage of the variance of each random effect divided by the total variance explained by all random effects) by the random effects. All evaluated models included bird identity, year and breeding colony as random effects.

Date of arrival at the breeding colony of migratory and non-migratory males of Cory's shearwater			
(a) Fixed factors structure	AICc	ΔAICc	$AICc_{weight}$
Migratory	**949.5**	**0.0**	**0.702**
Non-breeding area	952.6	3.1	0.149
Migratory + Non-breeding area	952.6	3.1	0.149
Constant	972.0	22.4	0.000
(b) Fixed effects		Estimates	
Migratory males		68.3 (57.6, 79.9)	
Non-migratory males		46.4 (33.1, 59.1)	
(c) Random Effects	Variance ± SD	Random variance explained (%)	
Individual	98.1 ± 9.9	32.7	
Year	12.4 ± 3.5	4.1	
Colony	46.4 ± 6.8	15.5	
Residual	143.1 ± 12.0	47.7	

Table 3. Linear mixed models (LMMs) testing for potential effects of sex on the arrival date at the breeding colony of the non-migratory Cory's shearwaters from Veneguera. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; $AICc_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model is shown in bold. (b) Mean estimates (and 95% confidence intervals in parenthesis) of the fixed effects. (c) Variance (± SD) and random variance explained (calculated as the percentage of the variance of each random effect divided by the total variance explained by all random effects) by the random effects. All evaluated models included bird identity and year as random effects.

Date of arrival to the breeding colony of non-migratory Cory's shearwater			
(a) Fixed factors structure	AICc	ΔAICc	$AICc_{weight}$
Sex	**183.7**	**0.0**	**0.837**
Constant	187.0	3.3	0.163
(b) Fixed effects		Estimates	
Males		39.6 (26.5, 52.7)	
Females		44.6 (28.6, 60.5)	
(c) Random Effects	Variance ± SD	Random variance explained (%)	
Individual	18.8 ± 4.3	5.5	
Year	52.7 ± 7.3	15.4	
Residual	271.6 ± 16.5	79.2	

Some male and female Cory's shearwaters from Veneguera did not migrate and remained in the Canary Current, near the colony. We tested whether sex influenced the date of arrival at the breeding colony in these non-migratory birds. The most parsimonious LMM retained sex, and non-migratory males returned to the colony about 5 days earlier than non-migratory females (Table 3).

4.3.2.2 Wintering distribution

Scopoli's shearwaters wintered in three main areas: the Canary Current (16 males, 12 females), the Guinea and Equatorial Currents (considered as a single area based on their geographical proximity) (7 males, 15 females) and the Angola and Benguela Currents (merged due to geographical proximity and uniformity of stable isotope values of the S13 of the individuals using this area (t-test: δ^{15}N $t_{(16.807)}$= -1.1571 P= 0.263; δ^{13}C: $t_{(17.270)}$= 1.3909 P= 0.182) (12 males, 8 females). No difference was found in the use of the non-breeding areas by males and females (χ^2= 4.3, d.f.= 3, P= 0.230). For Cory's shearwater, we identified up to six non-breeding areas: the North Atlantic area (7 males, 0 females), the South Atlantic area (6 males, 4 females), Canary Current (14 males, 10 females), the Angola and Benguela Currents (merged due to geographical proximity and uniformity of stable isotope values of the S13 of the individuals using this area (t-test: δ^{15}N $t_{(3.187)}$= 0.5719 P= 0.605; δ^{13}C: $t_{(3.048)}$= 0.6692 P= 0.551) (78 males, 59 females), the Agulhas Current (9 males, 14 females) and the Brazil Current (2 males, 12 females). We found that male and female Cory's shearwaters did not exploit their non-breeding areas in a similar manner (χ^2 = 17.7, d.f.= 5, P= 0.003). More specifically, no female from Vila islet (Azores) wintered in the Benguela Current or the North Atlantic, while no male from this colony wintered in the Agulhas Current (χ^2 = 19.2, d.f.= 4, P <0.001). Moreover, no female from Montaña Clara (Canary Is.) wintered in the Canary Current or the South Atlantic, while no males wintered in the Agulhas and Brazil Currents (Table S7 in Supplementary Appendix) (χ^2= 9.7, d.f.= 4, *P*= 0.052). All Cape Verde shearwater individuals wintered in the Brazil Current throughout the study period (10 males, 14 females) (Figure 2).

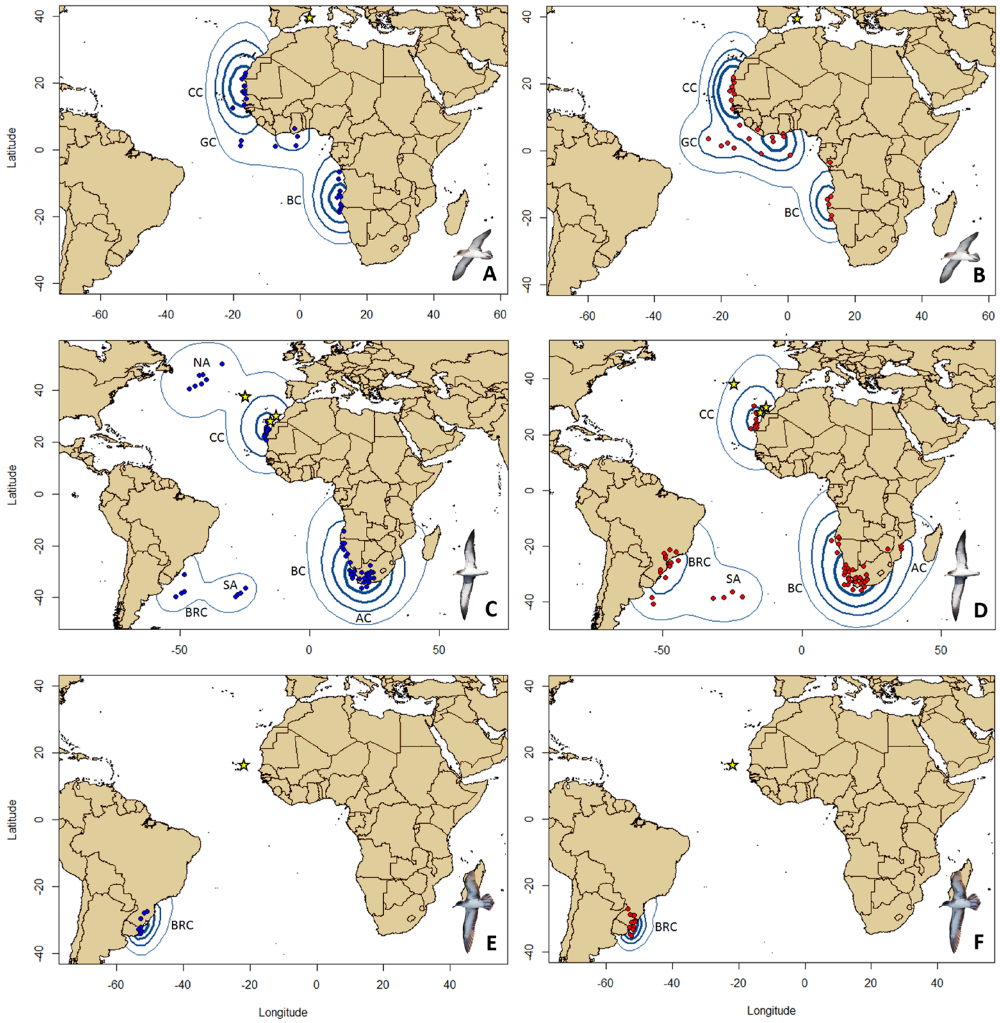

Figure 2. Non-breeding destinations of males (left, in blue) and females (right, in red) of Scopoli's (A, B), Cory's (C, D) and Cape Verde (E, F) shearwaters: AC = Agulhas Current, BC = Benguela Current, BRC = Brazil Current, CC = Canary Current, GC = Guinea Current, NA = North Atlantic and SA = South Atlantic. Dots represent the centroid of the non-breeding position of each individual and year (calculated as averaged coordinates of every 50% UD kernel). UD kernel (25, 50, 75 and 95%, from thicker to lighter blue line contours, respectively) for each sex and species are also depicted. Yellow stars represent the position of the breeding colonies. Note that, although filters were applied to geolocator data, a percentage of locations occurs on land because of the still relevant influence of the equinoxes. As a result, some individual centroids are on land, although we actually know shearwaters rarely travel inland. Note also that locations over the sea are subject to the same error rate as those on land, although, in this case, it is difficult to recognise.

Regarding the size of the core areas of the wintering distribution, most parsimonious LMM retained sex as explanatory factor (Table S9 in Supplementary Appendix). In general, females used a greater core area than males ($\text{mean}_{\text{males}}$= 618,646 km^2 [365,730 - 871,560], $\text{mean}_{\text{females}}$= 806,545 km^2 [553,630 – 1,059,460]). For most years and non-breeding areas, females of Scopoli's and Cory's shearwaters globally used a greater core area than males within each non-breeding area. In contrast, males of Cape Verde shearwater showed larger core areas in the Brazil Current during the two years studied (Table S8 in Supplementary Appendix). Finally, both sexes showed a high degree of overlap in their general use areas (95% Kernel density contours) and in the core areas (50% Kernel density contours) for most non-breeding areas and years (Table S10 in Supplementary Appendix).

4.3.2.3 At-sea behaviour

NFI revealed differences among sexes and species. Our model suggested that the females of Scopoli's and Cape Verde shearwaters tended to be more active during the night than males. Cory's shearwaters presented the opposite pattern and, overall, this species was more active at night than the other two (Table S11 in Supplementary Appendix).

4.3.3. Trophic ecology

4.3.3.1. Stable isotope analysis (SIA)

Overall, the S13 of the males of the three species showed slightly higher values of δ^{13}C ($\text{Mean estimates}_{\text{males}}$= -15.6 [-16.2, -15.1]) and δ^{15}N ($\text{Mean estimates}_{\text{males}}$= 14.0 [12.8, 15.3]) than in females ($\text{Mean estimates}_{\text{females}}$= -15.8 [-16.3, -15.3]) and 13.5 [12.3, 14.7] for δ^{13}C and δ^{15}N values, respectively) (Figure 3 and Table 4).

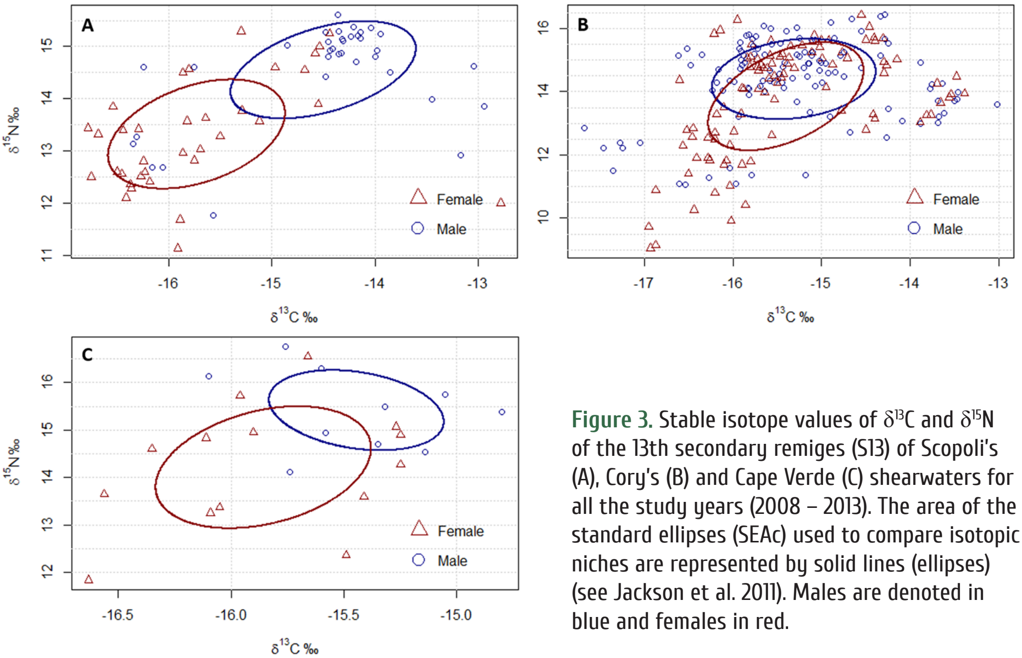

Figure 3. Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ of the 13th secondary remiges (S13) of Scopoli's (A), Cory's (B) and Cape Verde (C) shearwaters for all the study years (2008 – 2013). The area of the standard ellipses (SEAc) used to compare isotopic niches are represented by solid lines (ellipses) (see Jackson et al. 2011). Males are denoted in blue and females in red.

The best models for explaining differences in $\delta^{13}C$ and $\delta^{15}N$ values included sex, species, their interaction, and bill size. Although all variables were retained in the best models (with exception of the interaction between sex and bill size), the relative importance and significance of sex (1.0) and species (1.0) were higher when comparing with bill size (0.3 and 0.4 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively) (Table 4). Thus, we performed separate pairwise comparisons, and despite the lack of statistical significance for all the three species, isotopic values were, in general, slightly higher in males (Mean estimates= 0.6 [0.3, 0.9], *P* <0.001 and Mean estimates= 0.9 [0.5, 1.4], *P* <0.001 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively). The mean values of $\delta^{13}C$ (Mean estimates= 1.1 [0.7, 1.5], *P* <0.001) and $\delta^{15}N$ (Mean estimates= 1.1 [0.5, 1.7], *P* <0.001) were significantly lower in females for Scopoli's shearwater. Isotopic values of Cory's shearwater were similar between sexes (Mean estimates= 0.2 [-0.2, 0.6], *P*= 0.272 and Mean estimates= 0.4 [-0.1, 1.0], *P*= 0.106 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively) and in Cape Verde shearwater, isotopic values were significantly lower in females, only when considering $\delta^{15}N$ (Mean estimates= 0.4 [-0.1, 0.9], *P*= 0.112 and

Table 4. Linear mixed models (LMMs) testing for potential effects of bill size (residuals of the linear regression of PC1 scores as function of sex) and species in the stable isotope values of $\delta^{13}C$ (A) and $\delta^{15}N$ (B). (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; $AICc_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious models and those with ΔAICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) with adjusted SE obtained after performing model averaging between the best-supported models with ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. All the performed models included bird identity, year and non-breeding area as random effects.

$\delta^{13}C$				$\delta^{15}N$			
(a) Fixed factors structure	AICc	ΔAICc	$AICc_{weight}$	**(a) Fixed factors structure**	AICc	ΔAICc	$AICc_{weight}$
Sex + Species + Sex:Species	**330.1**	**0.0**	**0.647**	**Sex + Species + Sex:Species**	**462.2**	**0.0**	**0.283**
Sex + Species + Bill size + Sex:Species	**331.9**	**1.8**	**0.260**	**Sex + Species + Bill size + Sex:Bill size**	**462.6**	**0.4**	**0.228**
Sex + Species + Bill size + Sex:Species + Sex:Bill size	334.0	3.9	0.091	**Sex + Species**	**463.0**	**0.8**	**0.191**
Sex + Species	343.2	13.1	0.001	**Sex + Species + Bill size + Sex:Species**	**463.4**	**1.3**	**0.150**
Sex + Bill size	344.1	14.0	0.001	Sex + Species + Bill size	464.6	2.4	0.086
Sex + Species + Bill size	345.4	15.3	0.000	Sex + Species + Bill size + Sex:Species + Sex:Bill size	465.3	3.1	0.059
Sex + Bill size + Sex:Bill size	345.5	15.4	0.000	Species + Bill size	473.0	10.8	0.001
Sex	345.9	15.8	0.000	Species	479.3	17.2	0.000
Sex + Species + Bill size + Sex:Bill size	346.5	16.4	0.000	Sex + Bill size	506.6	44.5	0.000
Species + Bill size	351.8	21.7	0.000	Sex + Bill size + Sex:Bill size	508.5	46.4	0.000
Species	365.1	35.0	0.000	Sex	538.4	76.2	0.000
Constant	368.4	38.3	0.000	Constant	554.7	92.5	0.000
Bill size	425.2	95.1	0.000	Bill size	596.3	134.1	0.000
(b) Fixed effects		Estimates		**(b) Fixed effects**		Estimates	
Males		-15.6 (-16.2, -15.1)		Males		14.0 (12.8, 15.3)	
Females		-15.8 (-16.3, -15.3)		Females		13.5 (12.3, 14.7)	
Scopoli's shearwater		0.7 (0.3, 1.2)		Scopoli's shearwater		-0.2 (-1.0, 0.5)	
Cape Verde shearwater		0.8 (-0.1, 1.6)		Cape Verde shearwater		4.9 (3.5, 6.2)	
Females:Scopoli's shearwater		-0.9 (-1.3, -0.5)		Females:Scopoli's shearwater		-0.6 (-1.2, 0.0)	
Females:Cape Verde shearwater		-0.2 (-0.8, 0.3)		Females:Cape Verde shearwater		-0.8 (-1.6, 0.1)	
Bill size		0.1 (-0.1, 0.2)		Bill size		0.1 (-0.1, 0.4)	
				Females:Bill size		-0.2 (-0.3, 0.0)	
c) Relative variance importance (%)				**c) Relative variance importance (%)**			
Sex		1.0		Sex		1.0	
Species		1.0		Species		1.0	
Sex:Species		1.0		Sex:Species		0.5	
Bill size		0.3		Bill size		0.4	
				Sex:Bill size		0.3	

Mean estimates= 1.2 [0.4, 1.9], P= 0.002 for δ^{13}C and δ^{15}N values, respectively). Mean δ^{15}N values for Cape Verde shearwaters were significantly higher than for the other species (Mean estimates= 4.9 [3.5, 6.2], P <0.001) (Table S12 in Supplementary Appendix).

The null model and the one including species best explained the Bayesian estimate of the standard ellipse area (SEAb) values. After performing model averaging, values of the SEAb differed among species – with Cory's shearwater presenting higher values, followed by Scopoli's shearwater –, but not between sexes or among the size of core areas of the wintering distribution, with Scopoli's shearwaters showing the broadest isotope niches [Mean estimates= 1.5 (0.9, 2.0)] (Tables S13 and S14 in Supplementary Appendix).

4.4. Discussion

By combining geolocation data and isotopic values of feathers collected over 6 years, we evaluated the sexual segregation (SS) in spatio-temporal distribution, at-sea behaviour and feeding ecology in three closely related seabird species during their non-breeding period. Migratory males of the three species arrived earlier than females at their breeding grounds, although differences were more subtle than expected (3 days earlier on average). Non-migratory Cory's shearwater males remained in areas close to the colony in a larger proportion than females and arrived at the breeding colonies earlier than migratory males and both non-migratory and migratory females, as was found in Catry et al. (2013). Such differences in migratory behaviour can be explained by differential roles in reproduction according to the arrival time hypothesis, where the earlier arrival of males confers an advantage in mate acquisition and territory defence (Kokko et al. 2006, Catry et al. 2013, Hedd et al. 2014). Overall, males and females of the three *Calonectris* species did not differ in their spatial distribution and shared their main non-breeding areas, except for a specific wintering area of Cory's shearwater located NW of the Azores archipelago, apparently only used by males. Furthermore, males and females did not differ in their spatial distribution when sharing a given non-breeding area (i.e., at medium geographical scale), which would exclude hypotheses related to social dominance occurring during this period. In all three species, males generally showed greater values of $\delta^{13}C$ and $\delta^{15}N$ compared to females, although such differences were not always statistically significant. Given that the distribution within each non-breeding area did not differ between sexes, this result cannot arise from geographic differences in baseline isotopic levels, but suggests a subtle SS in trophic level and diet. However, we cannot be conclusive in this regard.

Spatio-temporal segregation between males and females

We found some sexual differences in the timing of migratory movements in the three species and in the use of non-breeding areas in Cory's shearwater. Only Cory's shearwater males from Vila, and a larger proportion of males than females from Veneguera, remained in areas close to their respective colonies year-round. Furthermore, males of the three species departed earlier than females from their breeding colonies in autumn at the onset of the post-breeding migration. In most cases, males also arrived earlier than females at the breeding colony, although this difference might vary depending on species, non-breeding area and year.

The inter-sexual differences we found in the non-breeding distribution of Cory's shearwaters are similar to those previously found for the same species in the Selvagens Islands (Pérez et al. 2013). The social dominance hypothesis could explain these results, with individuals of the larger sex staying closer to the breeding grounds and forcing subordinates to migrate further away. However, in the Veneguera colony (Canary Islands), for which we had a larger sample size, some females also did not migrate and wintered in the Canary Current, near the breeding colony. Furthermore, all areas, except the area NW of the Azores, were shared by males and females and we found no segregation between sexes in the spatial distribution within each non-breeding area for any of the species we considered. Similarly, Pérez et al. (2013) found no association between body size and the decision to migrate or remain resident in Cory's shearwater. Body size can be ruled out when explaining sexual differences in migration patterns and our results, therefore, do not support the social dominance hypothesis for explaining the sexual differences observed in the use of the non-breeding areas.

The arrival time hypothesis could explain both the greater tendency of Cory's shearwater males to remain resident and the slight, but consistent, phenological differences between sexes in the three species we studied. The early arrival of one sex at breeding grounds could be essential to ensure mating opportunities and the acquisition of suitable territories for breeding (Ketterson & Nolan 1983, Hedd et al. 2014). The earlier arrival of males occurs in many migratory bird species, while the opposite has been observed in only a few sex-role-reversed bird species (Reynolds et al. 1986, Kokko et al. 2006). In our study, sexual differences among migratory birds were more subtle than expected, since we found that migratory males arrived at breeding colonies only about 3 days earlier than migratory females on average. However, non-migratory males arrived approximately 23 days earlier than migratory males, and about 5 days earlier than non-migratory females, at their respective breeding colonies. Hence, despite the slight difference in the arrival dates among migratory birds, the pattern of males arriving at breeding colonies earlier than females has been consistent, being even more pronounced when males decide to remain resident. We suggest that the differences between migratory males and females are not so pronounced since the birds share the same non-breeding areas to winter, and the latitudes of non-breeding areas elected were related to the date of return to the breeding grounds. As previously observed in another study, the further shearwaters travelled from the colony, the later they returned to breed in the subsequent breeding period (Müller et al. 2015). In other studies, females wintered further south/north than males, and returned approximately 5 to 10 days later to breeding colonies (Catry et al. 2005, Phillips et al. 2005, Müller et al. 2014). Furthermore, the earlier departure of males from colonies for the post-breeding migration can be facultative since shearwaters are not territorial at sea and there may be no advantage in arriving at the non-breeding areas earlier than potential competitors (Kokko 1999). However, our results are consistent with those of Müller et al. (2015), who have suggested that Scopoli's shearwater males leave the breeding areas earlier than females so they can arrive earlier in the subsequent reproductive season, in a kind of "domino effect" (Briedis et al. 2019). According to the "domino effect", the timing of one phase of the annual cycle may affects the timing of the subsequent phase (Gow et al. 2019, Briedis et al. 2019), in this case, between post-breeding migration and arrival at the breeding colony for the subsequent reproductive season. Furthermore, although both sexes contribute equally to incubation and chick rearing (Hamer et al. 2002), males tend to spend more time and energy defending the nests at the beginning of the breeding period, which could also explain their earlier arrival (Hedd et al. 2014, Werner et al. 2014). Hence, sex differences in migration distance and timing may be better explained by the different roles in reproduction between males and females (Catry et al. 2005).

Sexual differences in at-sea behaviour and feeding ecology

Our results concerning at-sea behaviour and feeding ecology could be considered consistent with the ecological specialization hypothesis. In the three species, $\delta^{13}C$ and $\delta^{15}N$ values of the S13 remige (moulted during the non-breeding season) were slightly higher in males than in females. In seabirds, sexual differences in isotope ratios are often documented during different stages of the breeding period, but do not necessarily remain consistent year-round (Phillips et al. 2011, Phillips et al. 2017). The slight differences between sexes in δ^{13}C and δ^{15}N values found in our study suggest a small dietary segregation between sexes of the three species during the non-breeding period. These variations may occur due to differences in the metabolic rates between males and females (González-Solís et al. 2000). However, the extent to which metabolic rates affect species with slight SSD, such as *Calonectris* shearwaters, is poorly known. We also recognize that other factors not considered in this study, such as age, may influence metabolic rates (Alonso et al. 2012). Furthermore, sexual differences in δ^{13}C and δ^{15}N values could reflect different S13 remige moulting strategies among males and females, which occurs during the non-breeding period (Ramos et al. 2009c). Nevertheless, no differences were found in the onset of the molt of the primary remiges of Cory's shearwater males and females during the late chick-rearing period (Alonso et al. 2009), and further investigation into sexual differences in moulting schedules is required. Hence, we argue that at the end of the breeding period, when rearing duties are more relaxed and shearwaters can disperse over wider areas (Shaffer et al. 2006, González-Solís et al. 2007), foraging niches may better reflect intrinsic, sex-specific feeding preferences that may persist throughout the entire non-breeding period (Clay et al. 2016).

Differences in carbon isotope ratios are frequently used to determine differences between terrestrial versus marine ecosystems, inshore versus offshore and pelagic versus benthic food webs (Quillfeldt et al. 2005). We did not detect a clear spatial segregation between males and females within each non-breeding area, however females make use of a greater core area (50% KUD) than males, which may suggest that males forage more efficiently than females (Weimerskirch et al. 1997), as females need to forage in a larger area than males to ensure their requirements. Furthermore, higher δ^{13}C values in males, particularly in Scopoli's shearwaters, may suggest that males feed more heavily on the benthic prey (with higher $\delta^{13}C$ values) available at the surface layer in more central areas of the upwelling systems, whereas females feed in more peripheral areas, probably taking advantage of lesser quality food resources, with lower $\delta^{13}C$ values. The diet of *Calonectris* shearwaters during the non-breeding period is almost unknown (Barrett et al. 2007, Petry et al. 2009). In general, these shearwaters are shallow divers and tend to feed on surface prey during daylight (McNeil et al. 1993, Dias et al. 2012b, Grémillet et al 2014, Cianchetti-Benedetti et al. 2017), although both Scopoli's and Cory's shearwaters may also forage at night (Dias et al. 2012b, Rubolini et al. 2015). When in productive waters of non-breeding areas, birds may make use of the sit-and-wait foraging strategy, and food availability may be improved by the activities of subsurface predators and fisheries (Péron et al. 2010, Phillips et al. 2017). The more intense activity at night among female *Calonectris* shearwaters may suggest that they take greater advantage of the diel vertical migration of some mesopelagic fish, crustaceans and squids (lower trophic level prey characterized by lower $\delta^{15}N$ values) than males do (Hays 2003, Spear et al. 2007). In addition, sexual differences in the at-sea activity patterns and in isotopic values may also result from males exploiting more fishery discards than females (Hobson et al. 1994, Ramos et al. 2009b), which are often dominated by inshore benthonic species with higher $\delta^{13}C$ and $\delta^{15}N$ values (Hobson et al. 1994, Bugoni et al. 2011). The interactions of Scopoli's shearwaters with longline fisheries increase when the density of the fleet of operating trawlers is lower (and consequently, less discards are available) in the western Mediterranean (Soriano-Redondo et al. 2017), confirming that fisheries modify the natural way in which seabirds look for resources. Furthermore, the bycatch of Scopoli's shearwaters by longline fisheries in this area is male-biased, especially during the pre-laying period (Cortés et al. 2018).

In sexually dimorphic species, we might expect sexual differences in diet to be the result of different body sizes and, in particular, different sizes of feeding structures, such as the bill in birds (Amadon 1959, Selander 1966). Males are larger than females in the three shearwater species considered in this study, particularly with respect to bill size. We found a slight effect of bill measurements on the isotopic differences between sexes, which may suggest that at least some males are capable of feeding on larger prey at higher trophic levels (i.e., with higher $\delta^{15}N$ values) (Cherel & Hobson 2005). Previous studies conducted on Cory's shearwaters concluded that SSD in bill and wing dimensions were poor predictors of the way males and females exploit the marine environment (Navarro et al. 2009, Ramos et al. 2009a). Thus, the role of sexual selection in sexual differentiation in bill size in *Calonectris* shearwaters remains unclear, and results suggest the need to investigate the effect of individual body and bill size once controlled for sex.

Conclusions

In summary, Cory's shearwater males preferred to remain closer to the breeding grounds during the non-breeding period compared to females. Sex-related differences in several parameters of the migration phenology were also found, with males leaving and arriving earlier than females at the breeding grounds. This could be attributed to differential reproductive roles, in particular to the greater involvement of males in nest defence, rather than to male social dominance. This was supported by the apparent absence of spatial segregation between males and females within all main non-breeding areas, though this finding should be viewed with some caution due to the lack of fine-scale spatial resolution of the geolocators. Nevertheless, we observed some differentiation between sexes in nocturnal flight behaviour, with males displaying more diurnal flying activity than females in general. This finding was supported by isotopic values, which could reflect differences in feeding preferences and diet composition. However, trophic segregation was not fully supported by the SSD in bill size. Overall, our study showed that SS in ecological niche in seabirds persists year-round consistently but at a different extent. Based on our findings, and the fact that most of the studies conducted during the breeding period have reported sexual differences in the stable isotope values, we hypothesized that males and females might have evolved in exploiting different ecological niches as a result of an ecological specialization derived from differential reproductive roles (rather than from social dominance), which may persist throughout the annual cycle.

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Supplementary Appendix (at the end of the thesis)

Table S1. Proportion of variance explained by the different axes of the PCA conducted on culmen length, maximum head length, bill depth at the base and bill depth at nostrils representing an index of bill size.

Table S2. Accepted and mean measured (± SD) values of the standard material used in the stable isotope analysis performed in this study, as well as the mean minimum and maximum values obtain. The "n" refers to the number of samples of standards materials used.

Table S3. Mean values (± SD) of five biometric measurements of three *Calonectris* species: tarsus length, culmen length, maximum head length, bill depth at base and bill depth at nostrils and PC1 scores (as a proxy of bill size). (n) Number of measured Scopoli's, Cory's and Cape Verde shearwater individuals.

Table S4. Sexual size dimorphism index (SSI; Storer's index, see Materials and Methods) in biometric measurements and multivariate (PC1 scores) bill measurements of three *Calonectris* shearwaters.

Table S5. Linear mixed models (LMMs) testing for sex and species effects on seven migratory parameters in the three *Calonectris* species. (a) Structure of the candidate models evaluated to explain our data and values of Akaike's Information Criterion adjusted for small sample sizes (AICc). The most parsimonious model, and the models with ∆AICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) obtained from the best models and performing model averaging between the best-supported models when ∆AICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. (d) Estimated variance (± SD) of random effects of models in which we did not perform model averaging. All evaluated models included bird identity, year and non-breeding area as random effects.

Table S6. Linear mixed models (LMMs) testing for sex and species effects on the maximum distance travelled from the colony to the centroids of the non-breeding areas in the three *Calonectris* species. (a) Structure of the candidate models evaluated to explain our data and values of Akaike's Information Criterion adjusted for small sample sizes (AICc). The most parsimonious model, and the models with ∆AICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) obtained from the best models and performing model averaging between the best-supported models when ∆AICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. (d) Estimated variance (± SD) of random effects of models in which we did not perform model averaging. All evaluated models included bird identity, year and non-breeding area as random effects.

Table S7. Non-breeding destinations of males and females of Cory's shearwater separated by breeding colony.

Table S8. Sizes of wintering core areas (km^2) for males and females of Scopoli's, Cory's and Cape Verde shearwaters grouped by non-breeding area and year (minimum number of birds = 4). Core area sizes were calculated based on the 50% UD kernel contour for each sex, non-breeding area and year.

Table S9. Linear mixed models (LMMs) testing for potential effects of sex and species on the mean size of wintering core areas (calculated based on the 50% UD kernel contour for each sex, non-breeding area and year) of the three *Calonectris* species during the non-breeding period. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ∆AICc: AICc increments of each model in comparison with the best model; $\text{AICc}_{\text{weight}}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model is shown in bold. (b) Mean estimates (and 95% confidence intervals in parenthesis) of the fixed effects. (c) Variance (± SD) and random variance explained (calculated as the percentage of the variance of each random effect divided by the total variance explained by all random effects) by the random effects. All evaluated models included year and non-breeding area as random effects.

Table S10. Spatial overlap of the general use and wintering core areas of males and females of the three *Calonectris* species. Sizes of the general use and wintering core areas were calculated based on the 95% and 50% KUD contour, respectively, for each sex, non-breeding area and year (minimum number of birds = 4).

Table S11. Linear mixed models (LMMs) testing for potential effects of sex and species on the night flight index (NFI) of the three *Calonectris* species during the non-breeding period. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ∆AICc: AICc increments of each model in comparison with the best model; $\text{AICc}_{\text{weight}}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model, and the models with ∆AICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) obtained when performing model averaging between the best-supported models with ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. All evaluated models included bird identity and year as random effects.

Table S12. Post-hoc pairwise comparisons based on the difference between the least square means (and 95% confidence intervals in parenthesis) of the parameters of the most parsimonious models testing the effects of sex, species and bill size on δ^{13}C (A) and δ^{15}N (B) values of the S13 remige. Statistically significant results marked in bold are in relation to the significance level calculated using the Bonferroni correction ($P < 0.002$). All the models included bird identity, year and non-breeding area as random effects.

Table S13. Bayesian estimates of the standard ellipse areas (SEAb, ‰^{2}) ± SD (in parenthesis) for the values of δ^{13}C and δ^{15}N of the S13 remige of males and females of the three *Calonectris* species for each non-breeding area and year (we only considered non-breeding areas containing a minimum of 4 birds per sex and year).

Table S14. Linear mixed models (LMMs) testing for sex, species and the size of the core area of wintering distribution effects on the Bayesian estimate of the standard ellipse area (SEAb) used as an approach to characterize the isotope niche widths (INW) of the three *Calonectris* species. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; AICc$_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model, and the models with ΔAICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) with adjusted SE obtained after performing model averaging between the best-supported models with ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. All evaluated models included non-breeding area and year as random effects.

Chapter 5

GENERAL DISCUSSION

5

General discussion

This thesis aimed to understand causes and consequences of sexual segregation in spatio-temporal distribution, migratory phenology, at-sea behaviour and feeding ecology of three closely-related shearwaters: Scopoli's, Cory's and Cape Verde shearwaters (*Calonectris diomedea, C. borealis* and *C. edwardsii*, respectively) during the non-breeding period, and Scopoli's shearwater during the breeding period. We adopted a multidisciplinary approach combining geolocation, immersion data, GPS-tracking, spatial modelling and SIA to assess potential sexual differences within or between breeding and non-breeding periods, and in case they exist, to study whether they persist throughout the annual cycle and which are their main drivers. The thesis demonstrates that spatial segregation between males and females occur only during the breeding period for Scopoli's shearwater, in particular when shearwaters need to deal with unfavourable environmental conditions. The migratory phenology is consistently different between sexes for the three *Calonectris* shearwaters, males arriving earlier than females to breeding colonies and showing a greater tendency to remain resident around breeding grounds, likely due to sex-specific reproductive roles at early stages of the breeding period (Ketterson & Nolan 1983, Morbey & Ydenberg 2001). Sexes show consistent differences in SIA, which persisted year-round, and this probably relates to dietary specialization. Lastly, male Scopoli's shearwaters attended on fishing vessels twice more than females, probably due to an exclusive behaviour when competing for food resources, which agrees with the male-biased bycatch reported in the North-Western Mediterranean (NWM) (Cortés et al. 2018).

5.1. Spatio-temporal segregation between males and females

During the breeding period, parents are spatially constrained in areas close to breeding colonies due to the central place foraging strategy of these shearwaters (Granadeiro et al. 1998, Magalhães et al. 2008, Cecere et al. 2013). The high density of individuals may generate prey depletion on these areas, the so-called Ashmole's halo (Ashmole 1963, Lewis et al. 2001, Phillips et al. 2007), and thus the potential for inter-sexual competition is high (Orians & Pearson 1979, Lewis et al. 2002, Pinet et al. 2012). Nevertheless, Sexual Segregation (SS) may be reduced or even vanish during the non-breeding period, since seabirds are not constrained by the colony attendance and therefore birds are less exposed to prey depletion from their conspecifics (Shaffer et al. 2006, Bost et al. 2009) and feeding demands are lower because birds do not have to feed the chick. Our studies showed that the SS in space between sexes occurred only during the breeding period for Scopoli's shearwater, when birds are constrained to the NWM waters, in particular, under unfavourable environmental conditions, which may intensify inter-sexual competition due to the prey scarcity (Oro et al. 2004, Paiva et al. 2013, Paiva et al. 2007). Under such circumstances, males tended to exclude females and force them to forage in waters surrounding the breeding colony, possibly outcompeting females to access higher trophic level prey (Paiva et al. 2017). In several seabird species, males are the larger sex and tend to be dominant over subordinates, which are induced to travel further away for food, especially when environmental conditions are poor and resources are scarce (Gauthreaux 1978, González-Solís et al. 2000, Lewis et al. 2002, Paiva et al. 2017). Therefore, a greater proportion of female Scopoli's shearwaters travelled further than males, extended their main foraging areas, and remained more days away from the breeding colony in order to procure food for chick provisioning and to replenish their own body reserves (Magalhães et al. 2008). This result suggests that competitive exclusion may shape the spatial distribution and foraging areas of male and female Scopoli's shearwaters during the breeding period (Hunt & Schneider 1987, Stewart et al. 2000).

During the non-breeding period, the non-breeding distribution did not differ between sexes for none of the three study species. The exception occurred in NW of the Azores archipelago, a non-breeding area only visited by Cory's shearwater males that did not migrate. Although we did not detect spatial segregation between males and females within each non-breeding area, we acknowledge that subtle segregation at a local scale might have remained undetected due to the inherent low spatial resolution of geolocators (i.e., *ca.* 200 km; Phillips et al. 2004b). Moreover, female Scopoli's and Cory's shearwaters used a larger area to forage within each non-breeding area than males, suggesting that males are able to forage more efficiently than females (Weimerskirch et al. 1997), and a lower foraging effort can ensure males to achieve a higher body condition index and daily mass gain (Paiva et al. 2017). Thus, we suggest that competitive exclusion does not occur to such a degree as to generate spatial segregation during the non-breeding period, since males and females of the three *Calonectris* shearwaters share the same areas at this time.

5.2. Sexual differences in the migratory phenology

Differences in the timing of migration between males and females can be influenced by the intra-sexual competition, sex-specific reproductive roles and individual tolerance to suboptimal environmental conditions (Kokko 1999, Morbey & Ydenberg 2001). Our results showed that males and females slightly differed in their migratory strategies and timing for the three *Calonectris* shearwaters. Males are often the larger sex and because they are the territory defenders and more socially dominant towards females, males are the most pressed to arrive early to the breeding grounds (protandry in ethology; Myers 1981, Ketterson & Nolan 1983), and tend to spend more time and energy defending the nests at the beginning of the breeding period (Granadeiro et al. 1998, Jouanin et al. 2001, Hedd et al. 2014, Werner et al. 2014). The early arrival may allow males to acquire suitable territories for breeding and increase their mate opportunities, which could insure breeding success (Ketterson & Nolan 1983, Morbey & Ydenberg 2001, Hedd et al. 2014). Furthermore, males are thought to have a better tolerance to adverse weather conditions, having a greater tendency to be resident. According to the arrival time hypothesis, individuals more pressed for an early arrival at the breeding grounds benefit more from wintering closer to their breeding grounds (Myers 1981, Ketterson & Nolan 1983), since the early arrival could ensure mating opportunities and favour breeding success. Hence, we considered that the arrival time hypothesis, was plausible to explain the earlier arrival of males at their breeding grounds, but also the greater tendency of male Cory's shearwaters to remain resident compared to females. Hence, our results suggests that sex differences in migratory strategies and timing can be explained by the different roles in reproduction between males and females, especially early in the breeding period when males tend to be more active than females.

5.3. Sexual differences in at-sea behaviour, feeding ecology and in the probability of interaction with fishing vessels in the NWM

In seabirds, inter-sexual differences in isotope ratios are often documented during different stages of the breeding period, but they do not necessarily remain year-round, suggesting that differences in diet may not be permanent (Phillips et al. 2011, Paiva et al. 2015, Phillips et al. 2017). Differences related to diet and feeding preferences can be related to a niche-partitioning between sexes in order to reduce inter-sexual competition for food during the breeding period (González-Solís et al. 2000). Alternatively, once SSD in body size and feeding structures are developed, these sexual differences can promote habitat or niche specialization, which may persist year-round regardless of the inter-sexual competition for food (Selander 1966, Cleasby et al. 2015). However, in this thesis the effect of SSD in bill size as a driver of sexual differences in the diet of *Calonectris* shearwaters was negligible, and further studies on the role of sexual selection in the differentiation of the bill size and shape in *Calonectris* shearwaters and its relation with feeding preferences and diet specialization are still required.

Our results showed that males and females did not differ in δ^{13}C during the breeding period, but males, particularly of Scopoli's shearwaters, showed slightly higher δ^{13}C than females during the non-breeding period. During the non-breeding period, females make use of larger areas to forage than males and probably feed on different prey. We speculate that males are probably feeding more heavily on benthic prey (with higher δ^{13}C) available at the surface layer of more central areas of the upwelling systems (i.e. fishery discards or benthic prey performing diel vertical migration), and females feed in more peripheral areas on lesser quality food resources. Moreover, according to the NFI, females showed a slightly greater activity at night than males, which also suggests that they feed on some mesopelagic fish, crustaceans and squids (prey characterized by lower trophic level) that perform diel vertical migration (Hays 2003, Spear et al. 2007).

Regarding to the δ^{15}N, males of the three *Calonectris* shearwaters consistently showed higher values than females in both, breeding and non-breeding periods, which suggests that males are feeding on prey with higher trophic level (one unity higher) than females for both periods. Male Scopoli's shearwaters also showed the broadest INW in different environmental conditions, probably indicating relevant differences in diet (Cherel & Hobson 2005). However, we found that male Scopoli's shearwaters attended twice times more on fishing vessels than females in the Chapter 1 and we also showed birds that interacted with fishing vessels showed higher δ^{15}N. Thus, a higher δ^{15}N and a broader INW in males may be related to a greater exploitation of fishery discards compared to females for the breeding period (Votier et al. 2010). According to our results, males could be outcompeting females from exploiting discards, as previously suggested in other studies (Collet et al. 2015, Cianchetti-Benedetti et al. 2018), and sexual differences in SIA may mostly emerge from differential consumption of fishery discards between males and females during that period.

During the breeding period both sexes of Scopoli's shearwater interacted with fishing vessels in all the studied years. Favourable environmental conditions resulted in higher probability of fishing vessel attendance by both sexes, probably because a greater abundance of fish in the environment generates higher amounts of discards (Louzao et al. 2011). Under such circumstances, highest discard rates may reduce competitive exclusion behind fishing vessels, allowing more females to increase discard consumption to similar levels of males. On the contrary, a lower activity of fishing fleets in years with unfavourable environmental conditions, probably implies a lower amounts of discards and therefore an increase in competence between males and females. Despite about 25% of trips interacted in some extent with fishing vessels, only around 1% of time foraging during a foraging trip corresponded to fishing vessel attendance on average. The results obtained in this thesis are in line with previous studies conducted with Scopoli's shearwater and other procellariform species, which also find the probability of attendance to fishing vessels can be considered relatively low (Granadeiro et al. 2011, Torres et al. 2013, Cianchetti-Benedetti et al. 2018). Hence, although our research cannot directly evaluate whether Scopoli's shearwater bycatch occurs in association with these fisheries, we reinforce the need for greater consideration of SS on conservation measures, since events related to bycatch may be brief and may involve a small proportion of individuals but can have a strong impact on population viability (Croxall et al. 2013). Thus differences in movement, distribution and behaviour may increase the vulnerability of one sex when in contact with anthropogenic impacts, such as bycatch.

The results obtained in this thesis agreed with a sex-specific diet specialization, since males consistently fed on prey from higher trophic level (i.e. higher $\delta^{15}N$) than females during the breeding and non-breeding periods, and differences in SIA may reflect differences in diet composition, since both sexes use the same areas to forage (Cherel & Hobson 2005, Bearhop et al. 2006). Moreover, the fact that female Scopoli's shearwaters expanded their foraging grounds under unfavourable environmental conditions during the breeding period, and female Scopoli's and Cory's shearwaters made use of a larger area to forage during the non-breeding period, suggest that males forage more efficiently than females (Weimerskirch et al. 1997), since males are able to meet their nutritional requirements with a lower foraging effort (Salamolard & Weimerskirch, 1993).

5.4. Final considerations

The results found in this thesis corroborated with previous studies conducted on *Calonectris* shearwaters, which found SS in several aspects of their spatial and feeding ecologies (Catry et al. 2013, Pérez et al. 2013, Müller et al. 2014, Müller et al. 2015, Paiva et al. 2017, Cianchetti-Benedetti et al. 2017, Cianchetti-Benedetti et al. 2018). Since this thesis covered the entire annual cycle of one of the three study species and some sexual differences in their ecology persisted year-round, we reinforced the fact that species with slight SSD also present well marked SS and that intrinsic and extrinsic factors may promote inter-sexual differences in both, breeding and non-breeding periods.

This thesis highlighted the importance of multi-year approaches considering how different environmental conditions affect SS in foraging strategies and behaviour of a given species. The alterations in the environmental conditions, even when such differences were not so pronounced, were crucial to detect the increasing inter-sexual competition under unfavourable environmental conditions in the NWM. Furthermore, in years with favourable environmental conditions, the amount of fishery discards available and, consequently, the interactions of Scopoli's shearwaters with fishing vessels increased, which may increase the exposure of shearwaters to bycatch on those years.

Finally, this thesis showed that the presence of fishing vessels affects the foraging strategies and behaviour of male and female Scopoli's shearwaters differently, potentially leading to a sex-biased susceptibility to bycatch. Despite our study was not able to evaluate the bycatch rate of the species, it is known that bycatch of Scopoli's shearwater is male-biased in the region (Cortés et al. 2018). Thus, we would like to reinforce that SS in distribution and foraging behaviour should be take into consideration when implementing specific conservation plans for Scopoli's shearwater in the region.

Chapter 6

CONCLUSIONS

6

Conclusions

- During the breeding period, females expanded their foraging ranges, covering longer foraging trips for both chick-provisioning and replenish their own body reserves, increasing their foraging effort under unfavourable environmental conditions. Males tend to exclude females from the areas closest to the breeding colony under such environmental conditions, since male and female Scopoli's shearwaters may be competing for limited food resources;

- Scopoli's shearwaters interacted more with fishing vessels in favourable environmental conditions, probably because a greater abundance of fish in the environment generates higher amounts of discards. The more individuals of Scopoli's shearwater interacted with fishing vessels the higher the trophic level and broader INW, confirming that the species are scavenging on fishery discards. Male Scopoli's shearwaters attended on fishing vessels twice more than females taking more profit of discards, but probably exposing them to a higher bycatch risk than females;

- Sexual differences in migratory phenology were subtle for the three *Calonectris* shearwaters, but males consistently arrived earlier to breeding colonies than females, and male Cory's shearwaters show a greater tendency to remain resident that their conspecific females. This result is likely due to the differences in reproductive roles at early stages of the breeding period;

- Males and females of the three *Calonectris* shearwaters shared the same main non-breeding areas, suggesting that competitive exclusion does not occur to such a degree as to generate spatial segregation during the non-breeding period. However, within each non-breeding area, females made use of larger areas to forage than males, suggesting that males could be able to forage more efficiently than females while wintering;

- The slightly intense at-sea activity at night during the non-breeding period suggest that female Scopoli's and Cory's shearwaters can take advantage of mesopelagic fish, crustaceans and squids performing diel vertical migrations. Males of the three *Calonectris* shearwaters consistently showed a lower foraging effort and fed on prey from higher trophic level than females, which agrees with an inter-sexual diet specialization which persisted year-round. Furthermore, during the breeding period, males Scopoli's shearwaters could be outcompeting females from exploiting fishery discards, and sexual differences in diet occurring during that period may mostly emerge from differential consumption of fishery discards.

Chapter 7

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7

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Chapter 8

SUPPORTING INFORMATION

Supplementary Appendix of Chapter 3

S1. Environmental variables

We extracted for each year the mean value of satellite-derived environmental data matching the dates of the breeding period of tracked birds. We first calculated the convex hull polygon encompassing the full movement range of birds. Then we used functions from R package xtractomatic (Mendelssohn 2018) to download 8-day composite raster data within previous polygons for sea surface temperature, sea surface temperature anomaly, chlorophyll a and net primary productivity. We next calculated the annual mean value of each. We also download the NAO time series from NOAA website (www.cpc.ncep.noaa.gov) to calculate the extended annual winter NAO (NAOw) by averaging the winter monthly values (December–March). We scaled and centred all variables and evaluated their correlation (see Fig. S1). As all variables were highly correlated, we finally decided to use only the scaled value of NAOw for parsimony.

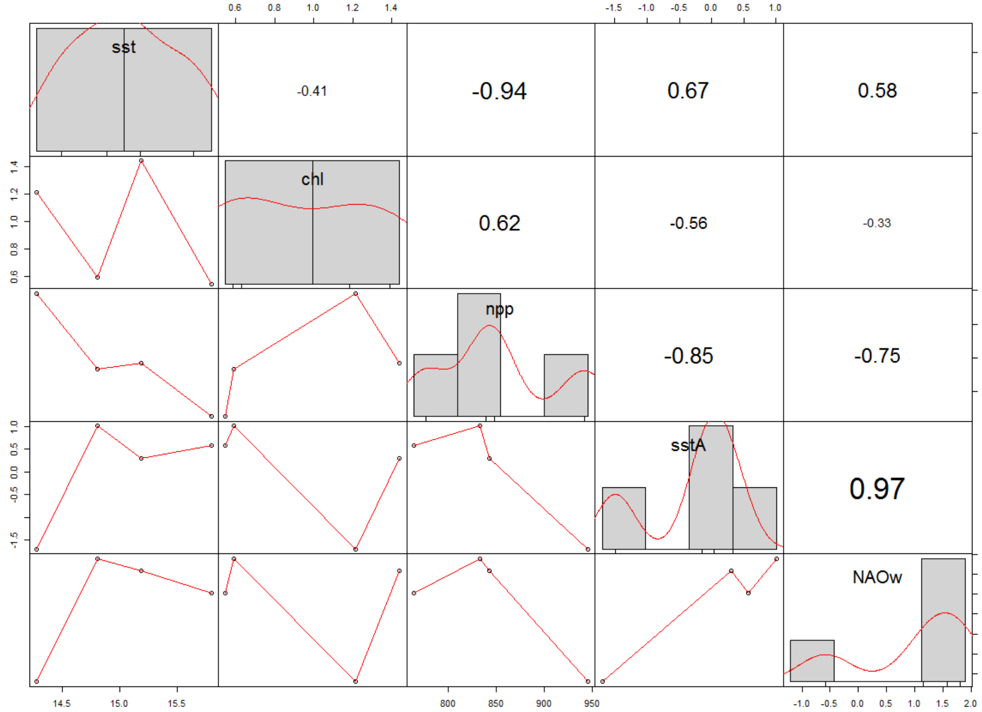


Figure S1. Correlation coefficients between environmental variables (mean of sea surface temperature (sst), mean of sea surface temperature Anomaly (sstA), mean of chlorophyll *a* concentration (chl), mean of net primary production (npp) and the extended annual winter NAO (NAOw) within the movement range of tracked birds.

S2. Stable isotope analysis (SIA) of plasma samples

We stored 1 ml of blood samples in a cold-preserved heparin-vial to be centrifuged within 12 h after collection. Later, we separated and froze plasma fractions at -20ºC for SIA. Once in the laboratory, plasma samples were lyophilized for 24h at 0 mBar and -50°C previous to homogenization. Each sample was homogenized with an Eppendorf mortar. We weighed 0.25 mg of each sample to the nearest µg (microbalance Mettler Toledo MX5), placed each sample in a tin capsule and crimpled them for combustion. Samples were oxidized ina Flash EA1112 coupled to a Delta-C isotope mass spectrometer through a Conflo III interface (Thermo Finnigan) to obtain $\delta^{13}C$ and $\delta^{15}N$ values. Isotope ratios are expressed as δ values in per mile (‰) related to the standard ratios (Viena Pee Dee Belemnite, VPDB for carbon and atmospheric nitrogen, AIR, for nitrogen). International standards (IAEA CH7, IAEA CH6 and USGS 40 for carbon and USGS 40, IAEA N1, IAEA NO3, IAEA N2 and IAEA 600 for nitrogen) were applied to calibrate and compensate for drift (Böhlke & Coplen 1995, Böhlke et al. 2003, Qi et al. 2003, Coplen et al. 2006) (Table S1). Replicated assays of these standards indicated a precision (SD) of 0.20 for carbon and 0.15 for nitrogen. For complex organic compounds such as plasma, however, these values are probably underestimated. It is known that lipid concentrations in plasma can lead to depleted $\delta^{13}C$ values (DeNiro & Epstein 1977, Cherel et al. 2005). Then, we calculated a correction value and applied to the $\delta^{13}C$ value of the samples. We selected randomly 20 samples previously analysed and performed lipid extraction to compare the $\delta^{13}C$ values. Plasma lipid extraction was performed by washing each sample with a solution of chloroform-methanol (2:1) (Bligh & Dyer 1959). The process was repeated until the supernatant was transparent, indicating that lipid extraction was complete. Finally, the samples were dried at 60°C for 24h and triturated with an Eppendorf mortar before weighing and laboratory analysing. With the values of carbon obtained after lipid extraction, we calculated a correlation between the relationship of the percentage of C and N with increasing $\delta^{13}C$ through SPSS® software. We corrected the values without lipid extraction according to the formula:

$$\delta^{13}C_{\text{corrected}} = -1.397 + 0.512 * C{:}N + \delta^{13}C,$$

where δ^{13}Ccorrected is the corrected value after performing the lipid extraction, C:N ratio is the carbon and nitrogen relationship percentage, and $\delta^{13}C$ is the isotopic value of samples without lipid extraction. The relationship between the C:N ratio and $\delta^{13}C$ value is practically linear with a R2 of about 0.2, a very low value which can increase $\delta^{13}C$ values in about 0.8-0.9‰. All the isotopic analyses were performed at the Isotopic Ratio Mass Spectrometry Facility of the University of Barcelona's Scientific and Technical Services.

Table S2. Accepted and mean measured (± SD) of the standard material used in the stable isotope analysis performed in this study, as well as the mean, minimum (Min) and maximum (Max) values obtained. The "n" refers to the number of samples of standards materials used.

International standards	δ^{15}NAir (‰)								δ^{13}CVPDB (‰)							
	Reference value		Observed value						Reference value		Observed value					
	Mean	SD	n	Min	Max	Mean	SD	Mean diff.	Mean	SD	n	Min	Max	Mean	SD	Mean diff.
IAEA CH6									-10.5	0.0	3	-10.9	-10.6	-10.8	0.2	0.3
IAEA CH7									-32.2	0.1	3	-32.3	-32.0	-32.2	0.1	0.0
IAEA 600	1.0	0.2	3	1.1	1.4	1.2	0.2	0.2	-27.8	0.0	3	-27.9	-27.3	-27.7	0.3	0.1
USGS 40	-4.5	0.1	3	-4.0	-3.9	-3.9	0.0	0.6	-26.2	0.1	3	-26.7	-26.5	-26.6	0.1	0.4
IAEA N1	0.4	0.1	3	0.3	1.0	0.7	0.4	0.3								
IAEA N2	20.4	0.1	3	19.3	20.0	19.6	0.4	0.9								
IAEA NO3	4.7	0.1	2	4.6	4.9	4.8	0.2	0.1								

S3. Space use by sex and year

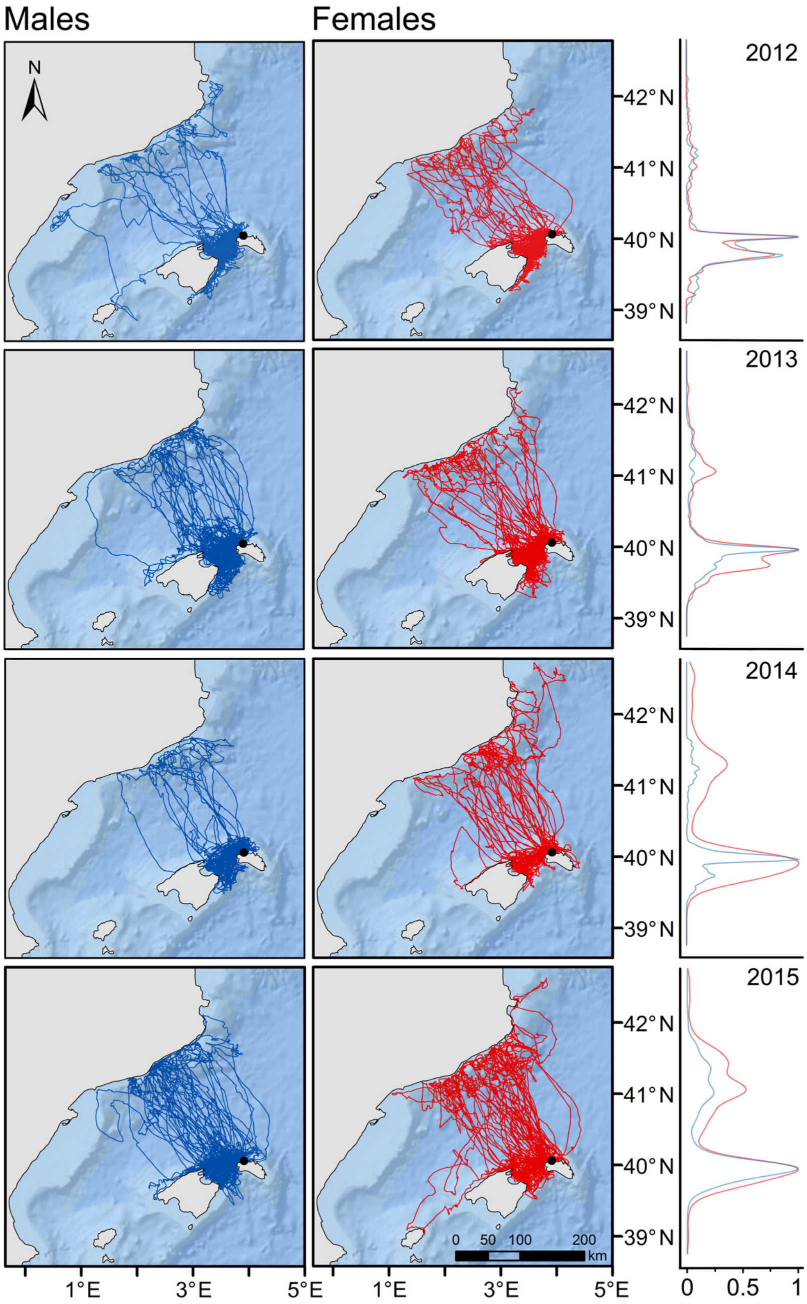
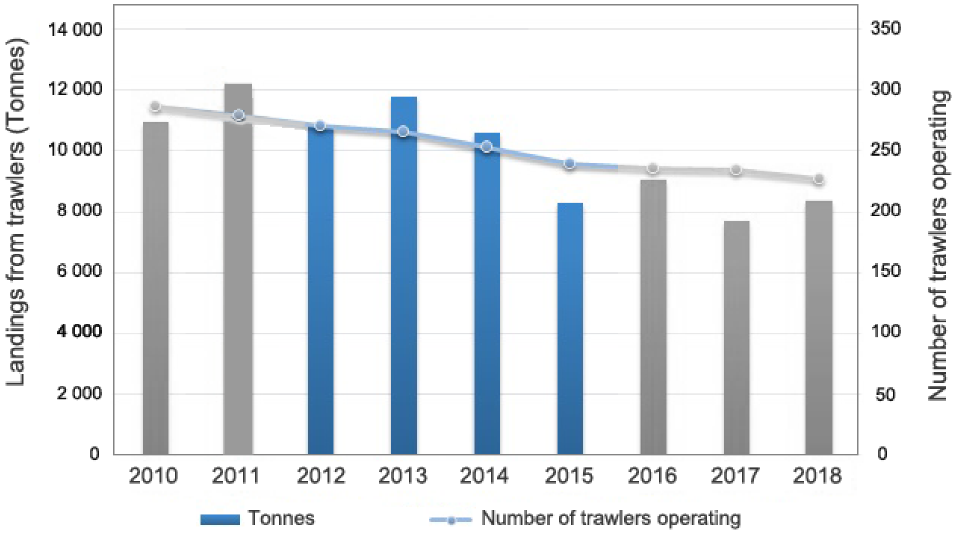


Figure S2. Trajectories recorded with GPS loggers showed by sex and year. The black circle represents the colony. Density plots in the right-side point out the bimodal strategy of birds, performing short trips to waters nearby the colony and long trips towards Catalan waters. The number of long trips, however, varied annually, especially in females, likely due to inter-annual variability in the environmental conditions.

S4. Fisheries



NAOw: 2012 = 1.04; 2013 = -1.20; 2014 = 1.60; 2015 = 1.89

Figure S3. Trawling landing (in Tonnes) and number of trawlers operating in Catalan waters (2010 to 2018). Original plot downloaded from http://agricultura.gencat.cat. Years included in this study (2012-2015) are shown in blue. Previous studies have found a positive correlation between landing rates and the amount of discards in the North-Western Mediterranean (Louzao et al. 2011).

S5. Potential prey

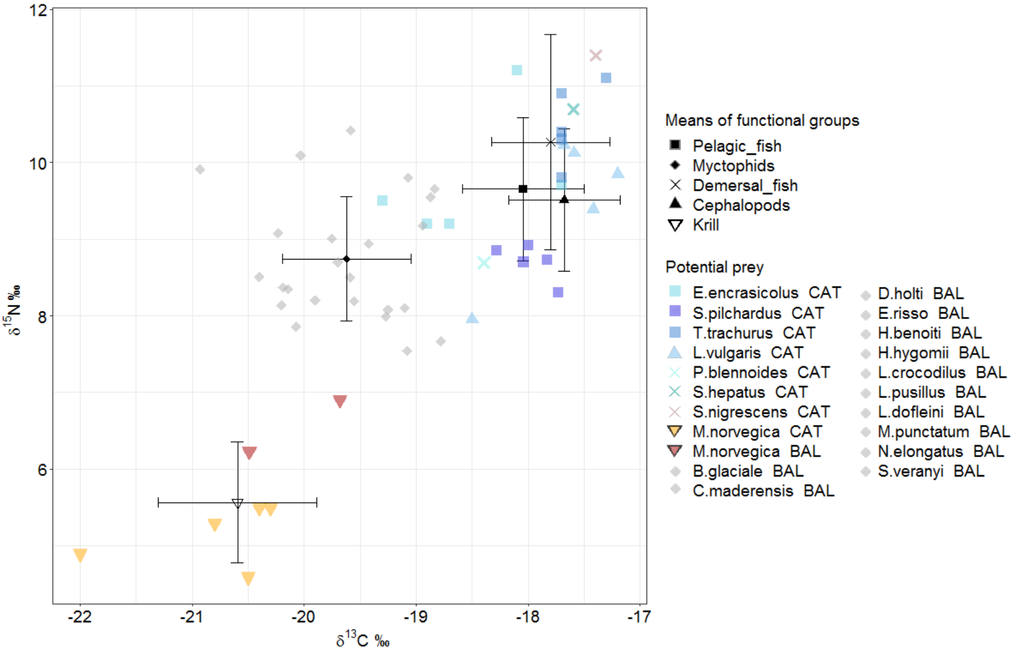


Figure S3. Biplot of δ^{15}N-δ^{13}C values of species considered as potential prey (length <15 cm) of Scopoli's shearwaters separated by area (BAL=Balearic waters; CAT=Catalan waters). The shape indicates the corresponding functional group. Error bars represent mean and standard deviation in δ^{13}C and δ^{15}N values of each functional group. Each dot corresponds to a sample from a single species and sampling area. Note that all myctophid species are represented with the same colour. Isotopic values were obtained from Navarro et al. (2009), Valls et al. (2014) and Cardona et al. (2015).

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Supplementary Appendix of Chapter 4

Table S1. Proportion of variance explained by the different axes of the PCA conducted on culmen length, maximum head length, bill depth at the base and bill depth at nostrils representing an index of bill size.

Importance of components:				
	PC1	PC2	PC3	PC4
Standard deviation	1.91	0.44	0.25	0.22
Proportion of variance	0.92	0.05	0.01	0.01
Cumulative proportion	0.92	0.97	0.98	1.00

Table S2. Accepted and mean measured (± SD) values of the standard material used in the stable isotope analysis performed in this study, as well as the mean minimum and maximum values obtain. The "n" refers to the number of samples of standards materials used.

Standard material name	$\delta^{15}N_{Air}$ (‰)				$\delta^{13}C_{VPDB}$ (‰)			
	Accepted value	Measured values			Accepted value	Measured values		
	Mean ± SD	n	Mean ± SD	Minimum - maximum	Mean ± SD	n	Mean ± SD	Minimum - maximum
IAEA CH6					−10.4 ± 0.0	21	−10.8 ± 0.3	−11.2 to -10.3
IAEA CH7					−32.2 ± 0.1	22	−32.2 ± 0.2	−32.5 to −31.7
IAEA 600	+1.0 ± 0.2	12	+0.8 ± 0.1	0.6 to 1.0	−27.8 ± 0.0	12	−27.8 ± 0.4	−28.2 to −27.2
USGS 40	−4.5 ± 0.1	24	−4.6 ± 0.1	−4.9 to −4.4	−26.2 ± 0.1	24	−26.5 ± 0.3	−27.1 to −26.0
IAEA N1	+0.4 ± 0.1	19	+0.3 ± 0.3	0 to 0.8				
IAEA N2	+20.4 ± 0.1	20	+19.7 ± 0.3	19.3 to 20.2				
IAEA NO3	+4.7 ± 0.1	9	+4.4 ± 0.3	3.7 to 4.8				
USGS 34	−1.8 ± 0.2	9	−1.9 ± 0.1	−2.0 to −1.8				

Table S3. Mean values (± SD) of five biometric measurements of three *Calonectris* species: tarsus length, culmen length, maximum head length, bill depth at base and bill depth at nostrils and PC1 scores (as a proxy of bill size). (n) Number of measured Scopoli's, Cory's and Cape Verde shearwater individuals.

Species	n		Tarsus (mm)		Maximum head length (mm)		Culmen length (mm)		Bill depth at base (mm)		Bill depth at nostrils (mm)		PC1 scores	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Scopoli's shearwater	21	22	55.4 ± 1.8	53.1 ± 1.8	109.3 ± 3.9	102.8 ± 3.9	52.2 ± 2.2	49.0 ± 2.2	19.8 ± 1.5	17.3 ± 1.5	14.5 ± 1.0	12.7 ± 1.0	-0.6 ± 1.3	1.2 ± 1.3
Cory's shearwater	44	40	58.0 ± 2.0	56.0 ± 2.1	114.1 ± 3.9	109.8 ± 3.9	55.3 ± 2.3	52.5 ± 2.1	21.6 ± 1.3	19.6 ± 1.4	15.7 ± 1.0	14.4 ± 1.0	-2.0 ± 1.3	-0.6 ± 1.2
Cape Verde shearwater	7	10	49.4 ± 1.8	46.5 ± 1.8	95.0 ± 2.5	91.3 ± 3.0	45.1 ± 1.8	42.7 ± 2.1	15.7 ± 1.0	14.6 ± 1.0	11.9 ± 1.7	10.6 ± 1.6	2.7 ± 0.8	3.8 ± 0.9

Table S4. Sexual size dimorphism index (SSI; Storer's index, see Materials and Methods) in biometric measurements and multivariate (PC1 scores) bill measurements of three *Calonectris* shearwaters.

Species	n	Tarsus	Maximum head length	Culmen length	Bill depth	Bill depth at nostril	PC1 score
Scopoli's shearwater	43	4.2	6.2	6.4	13.4	13.3	0.3
Cory's shearwater	84	3.4	3.9	5.2	9.8	8.4	-1.4
Cape Verde shearwater	17	6.0	4.0	5.3	7.8	11.8	3.4

Table S5. Linear mixed models (LMMs) testing for sex and species effects on seven migratory parameters in the three *Calonectris* species. (a) Structure of the candidate models evaluated to explain our data and values of Akaike's Information Criterion adjusted for small sample sizes (AICc). The most parsimonious model, and the models with ΔAICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) obtained from the best models and performing model averaging between the best-supported models when ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. (d) Estimated variance (± SD) of random effects of models in which we did not perform model averaging. All evaluated models included bird identity, year and non-breeding area as random effects.

	Departure from the breeding colony (Julian date)	Days in transit to the non-breeding areas	Total duration of the non-breeding period (in days)	Days in non-breeding areas	Onset of the pre-breeding migration (Julian date)	Days in transit to the breeding colony	Arrival at the breeding colony (Julian date)
(a) Fixed factors structure (AICc)							
Sex + Species + Sex:Species	2354.7	1868.3	2463.4	2396.3	2152.9	1954.3	2181
Sex + Species	**2351.1**	1864.1	**2459.3**	**2393.0**	**2150.1**	**1952.3**	2179.4
Sex	2378.1	1878.8	2472.3	2425.8	2158.0	1972.3	**2175.1**
Species	**2352.2**	**1862.0**	**2457.5**	**2391.8**	**2148.2**	1954.6	2179.4
Constant	2378.5	1876.7	2470.6	2425.0	2156.0	1973.4	**2175.2**
(b) Fixed effects (Estimates)							
Males	316.4 (312.5, 320.5)		113.7 (107.6, 119.5)	61.3 (52.5, 70.2)	44.6 (41.2, 47.9)	20.8 (19.0, 22.6)	65.7 (59.4, 71.8)
Females	321.1 (317.0, 325.2)		111.9 (106.0, 118.1)	58.9 (50.1, 67.6)	45.4 (42.1, 48.9)	23.1 (21.3, 25.0)	68.3 (62.2, 74.4)
Cory's shearwater	318.7 (314.8, 322.6)	14.8 (12.0, 17.5)	112.8 (107.9, 117.8)	60.1 (51.4, 68.8)	45.0 (42.0, 48.0)	22.0 (20.4, 24.0)	
Scopoli's shearwater	298.7 (295.0, 302.4)	8.8 (7.1, 9.7)	129.1 (122.9, 135.2)	79.3 (66.8, 91.8)	49.2 (46.3, 52.1)	14.0 (12.0, 16.0)	
Cape Verde shearwater	320.3 (317.5, 323.9)	10.9 (9.1, 11.2)	114.9 (109.5, 118.3)	80.5 (73.8, 87.2)	55.0 (51.5, 58.6)	13.9 (11.7, 16.5)	
(c) Relative variance importance (%)							
Sex	0.6		0.3	0.4	0.3		0.5
Species	1.0		1.0	1.0	1.0		
Sex:Species							
(d) Random effects (variance ± SD)							
Individual		0.0 ± 0.0				8.9 ± 3.0	
Year		4.2 ± 2.1				0.7 ± 0.8	
Non-breeding area		4.4 ± 2.1				0.0 ± 0.0	

Table S6. Linear mixed models (LMMs) testing for sex and species effects on the maximum distance travelled from the colony to the centroids of the non-breeding areas in the three *Calonectris* species. (a) Structure of the candidate models evaluated to explain our data and values of Akaike's Information Criterion adjusted for small sample sizes (AICc). The most parsimonious model, and the models with ΔAICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) obtained from the best models and performing model averaging between the best-supported models when ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. (d) Estimated variance (± SD) of random effects of models in which we did not perform model averaging. All evaluated models included bird identity, year and non-breeding area as random effects.

Maximum distance travelled from the colony to the centroids of the non-breeding areas			
(a) Fixed factors structure	AICc	ΔAICc	$AICc_{weight}$
Non-breeding area	**712.2**	**0.0**	**0.457**
Species + Non-breeding area	**713.2**	**1.0**	**0.275**
Sex + Non-breeding area	714.3	2.1	0.161
Sex + Species + Non-breeding area	715.4	3.2	0.094
Sex + Species + Non-breeding area + Sex:Species	719.6	7.3	0.012
Sex + Species	1239.2	526.9	0.000
Species	1239.3	527.0	0.000
Sex + Species + Sex:Species	1241.9	529.7	0.000
Constant	1247.1	534.8	0.000
Sex	1247.1	534.9	0.000
(b) Fixed effects		Estimates	
Agulhas Current:Cory's shearwater		8.1 (7.5, 8.8)	
Benguela Current		-0.7 (-1.0, -0.3)	
Brazil Current		-1.0 (-1.5, -0.4)	
Canary Current		-6.1 (-6.6, -5.7)	
Guinea Current		-3.8 (-4.3, -3.2)	
North Atlantic		-7.3 (-8.1, -6.5)	
South Atlantic		-0.1 (-0.7, 0.5)	
Scopoli's shearwater		-0.1 (-1.1, 1.0)	
Cape Verde shearwater		-1.2 (-2.3, -0.1)	
(c) Relative variance importance (%)			
Non-breeding area		1.0	
Species		0.4	

Table S7. Non-breeding destinations of males and females of Cory's shearwater separated by breeding colony.

Breeding colony	Non-breeding area	n	
		Males	Females
Vila islet (Azores)	Agulhas Current	0	5
	Benguela Current	7	0
	Brazil Current	1	2
	North Atlantic Ocean	7	0
	South Atlantic Ocean	1	2
Montaña Clara (Canary Islands)	Agulhas Current	0	2
	Benguela Current	7	9
	Brazil Current	0	5
	Canary Current	1	0
	South Atlantic Ocean	2	0
Veneguera (Canary Islands)	Agulhas Current	9	7
	Benguela Current	64	50
	Brazil Current	1	5
	Canary Current	13	10
	South Atlantic Ocean	3	2

Table S8. Sizes of wintering core areas (km^2) for males and females of Scopoli's, Cory's and Cape Verde shearwaters grouped by non-breeding area and year (minimum number of birds = 4). Core area sizes were calculated based on the 50% UD kernel contour for each sex, non-breeding area and year.

Species	Non-breeding area	Year	Core area (km^2)			
			n Males	**Males**	n Females	**Females**
Scopoli's shearwater	Canary Current	2011	6	569,564	7	701,080
		2012	9	421,943	4	488,317
	Guinea Current	2012	6	1,308,328	5	1,465,092
	Benguela Current	2010	10	711,411	5	953,732
	Mean			**752,812**		**902,055**
Cory's shearwater	Canary Current	2012	5	467,507	4	704,844
	Benguela Current	2008	9	1,141,296	8	1,279,964
		2009	11	562,722	6	628,410
		2010	8	769,852	10	759,279
		2011	18	178,743	5	466,224
		2012	22	994,756	21	1,027,324
		2013	9	651,885	6	647,138
	Mean			**680,966**		**787,598**
Cape Verde shearwater	Brazil Current	2010	4	632,719	5	613,933
		2011	4	526,576	4	438,259
	Mean			**579,648**		**526,096**

Table S9. Linear mixed models (LMMs) testing for potential effects of sex and species on the mean size of wintering core areas (calculated based on the 50% UD kernel contour for each sex, non-breeding area and year) of the three *Calonectris* species during the non-breeding period. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; $AICc_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model is shown in bold. (b) Mean estimates (and 95% confidence intervals in parenthesis) of the fixed effects. (c) Variance (± SD) and random variance explained (calculated as the percentage of the variance of each random effect divided by the total variance explained by all random effects) by the random effects. All evaluated models included year and non-breeding area as random effects.

Mean size of wintering core areas			
(a) Fixed factors structure	**AICc**	**ΔAICc**	**$AICc_{weight}$**
Sex	**887.8**	**0.0**	**0.592**
Constant	890.1	2.3	0.192
Sex + Species	890.6	2.7	0.150
Species	892.8	4.9	0.050
Sex + Species + Sex:Species	895.1	7.3	0.015
(b) Fixed effects	Estimates		
Males	806.5 (553.6, 1059.5)		
Females	618.6 (365.7, 871.6)		
(c) Random Effects	Variance ± SD	Random variance explained (%)	
Non-breeding area	70478 ± 265.5	38.6	
Year	1627 ± 40.3	0.9	
Residuals	110596 ± 332.6	60.5	

Table S10. Spatial overlap of the general use and wintering core areas of males and females of the three *Calonectris* species. Sizes of the general use and wintering core areas were calculated based on the 95% and 50% KUD contour, respectively, for each sex, non-breeding area and year (minimum number of birds = 4).

Species	Non-breeding area	Year	Overlap	
			95% KUD	50% KUD
Scopoli's shearwater	Canary Current	2011	0.776	0.860
		2012	0.734	0.908
	Guinea Current	2012	0.460	0.235
	Benguela Current	2010	0.750	0.953
Cory's shearwater	Canary Current	2012	0.987	0.963
	Benguela Current	2008	0.902	0.718
		2009	0.452	0.281
		2010	0.811	0.581
		2011	0.475	0.763
		2012	0.644	0.931
		2013	0.894	0.786
Cape Verde shearwater	Brazil Current	2010	0.845	0.965
		2011	0.831	0.733

Table S11. Linear mixed models (LMMs) testing for potential effects of sex and species on the night flight index (NFI) of the three *Calonectris* species during the non-breeding period. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; $\text{AICc}_{\text{weight}}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model, and the models with ΔAICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) obtained when performing model averaging between the best-supported models with ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. All evaluated models included bird identity and year as random effects.

NFI			
(a) Fixed factors structure	AICc	ΔAICc	$\text{AICc}_{\text{weight}}$
Sex + Species + Sex:Species	**-103.8**	**0.0**	**0.501**
Sex + Species	**-102.9**	**0.9**	**0.317**
Species	-101.8	2.0	0.181
Constant	-73.4	30.4	0.000
Sex	-73.3	30.6	0.000
(b) Fixed effects		Estimates	
Males:Cory's shearwater (Intercept)		-0.3 (-0.4, -0.2)	
Females:Cory's shearwater		-0.4 (-0.5, -0.3)	
Scopoli's shearwater		-0.3 (-0.4, -0.2)	
Cape Verde shearwater		-0.2 (-0.4, -0.1)	
Females:Scopoli's shearwater		0.1 (0.0, 0.3)	
Females:Cape Verde shearwater		0.0 (-0.2, 0.2)	
(c) Relative variance importance (%)			
Sex		1.0	
Species		1.0	
Sex:Species		0.6	

Table S12. Post-hoc pairwise comparisons based on the difference between the least square means (and 95% confidence intervals in parenthesis) of the parameters of the most parsimonious models testing the effects of sex, species and bill size on $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values of the S13 remige. Statistically significant results marked in bold are in relation to the significance level calculated using the Bonferroni correction ($P < 0.002$). All the models included bird identity, year and non-breeding area as random effects.

A) $\delta^{13}C$

(a) Pairwise comparison	Estimates	*P*
Males – Females	0.6 (0.3, 0.9)	<0.001
Cory's – Scopoli's shearwater	-0.2 (-0.7, 0.3)	0.369
Cory's – Cape Verde shearwater	-0.4 (-1.4, 0.5)	0.359
Scopoli's – Cape Verde shearwater	-0.2 (-1.0, 0.6)	0.580
Males Cory's – Females Cory's	0.2 (-0.2, 0.6)	0.272
Males Cory's – Males Scopoli's	-0.7 (-1.2, -0.2)	0.006
Males Cory's – Females Scopoli's	0.4 (-0.3, 1.2)	0.223
Males Cory's – Males Cape Verde	-0.6 (-1.6, 0.5)	0.298
Males Cory's – Females Cape Verde	-0.1 (-1.3, 1.0)	0.811
Females Cory's – Males Scopoli's	-0.9 (-1.3, -0.4)	**<0.001**
Females Cory's – Females Scopoli's	0.2 (-0.3, 0.8)	0.401
Females Cory's – Males Cape Verde	-0.8 (-1.6, 0.1)	0.082
Females Cory's – Females Cape Verde	-0.3 (-1.3, 0.6)	0.480
Males Scopoli's – Females Scopoli's	1.1 (0.7, 1.5)	**<0.001**
Males Scopoli's – Males Cape Verde	0.1 (-0.8, 1.0)	0.788
Males Scopoli's – Females Cape Verde	0.5 (-0.5, 1.5)	0.293
Females Scopoli's – Males Cape Verde	-1.0 (-1.8, -0.2)	0.011
Females Scopoli's – Females Cape Verde	-0.6 (-1.4, 0.2)	0.164
Males Cape Verde – Females Cape Verde	0.4 (-0.1, 0.9)	0.112

B) $\delta^{15}N$

(a) Pairwise comparison	Estimates	*P*
Males – Females	0.9 (0.5, 1.4)	**<0.001**
Cory's – Scopoli's shearwater	0.6 (-0.2, 1.3)	0.122
Cory's – Cape Verde shearwater	-4.3 (-5.8, -2.9)	**<0.001**
Scopoli's – Cape Verde shearwater	-4.9 (-6.2, -3.7)	**<0.001**
Males Cory's – Females Cory's	0.4 (-0.1, 1.0)	0.106
Males Cory's – Males Scopoli's	0.2 (-0.5, 1.0)	0.510
Males Cory's – Females Scopoli's	1.4 (0.3, 2.4)	0.013
Males Cory's – Males Cape Verde	-4.7 (-6.3, -3.1)	**<0.001**
Males Cory's – Females Cape Verde	-3.5 (-5.3, -1.8)	**<0.001**
Females Cory's – Males Scopoli's	-0.2 (-0.9, 0.5)	0.568
Females Cory's – Females Scopoli's	0.9 (0.1, 1.8)	0.036
Females Cory's – Males Cape Verde	-5.1 (-6.4, -3.9)	**<0.001**
Females Cory's – Females Cape Verde	-4.0 (-5.4, -2.5)	**<0.001**
Males Scopoli's – Females Scopoli's	1.1 (0.5, 1.7)	**<0.001**
Males Scopoli's – Males Cape Verde	-5.0 (-6.3, -3.6)	**<0.001**
Males Scopoli's – Females Cape Verde	-3.8 (-5.3, -2.2)	**<0.001**
Females Scopoli's – Males Cape Verde	-6.1 (-7.2, -4.9)	**<0.001**
Females Scopoli's – Females Cape Verde	-4.9 (-6.1, -3.6)	**<0.001**
Males Cape Verde – Females Cape Verde	1.2 (0.4, 1.9)	**0.002**

Table S13. Bayesian estimates of the standard ellipse areas (SEAb, ‰^{2}) ± SD (in parenthesis) for the values of $\delta^{13}C$ and $\delta^{15}N$ of the S13 remige of males and females of the three *Calonectris* species for each non-breeding area and year (we only considered non-breeding areas containing a minimum of 4 birds per sex and year).

Species	Non-breeding area	Year	SEAb			
			Males (‰^{2})	**n**	**Females (‰^{2})**	**n**
Scopoli's shearwater	Guinea Current	2011	1.6 (0.7, 4.2)	6	0.5 (0.2, 1.2)	7
	Canary Current	2011	0.8 (0.4, 1.7)	9	1.1 (0.4, 3.8)	4
		2012	0.1 (0.0, 0.2)	6	0.5 (0.2, 1.6)	5
	Benguela Current	2010	0.8 (0.4, 1.5)	10	1.2 (0.4, 3.4)	5
Cory's shearwater	Canary Current	2012	0.4 (0.2, 1.4)	5	0.1 (0.0, 0.3)	4
	Benguela Current	2008	0.2 (0.1, 0.5)	9	0.7 (0.3, 1.7)	8
		2009	0.7 (0.4, 1.3)	11	0.4 (0.2, 1.1)	1.1
		2010	0.7 (0.3, 1.5)	8	1.1 (0.6, 2.1)	10
		2011	1.7 (1.1, 2.8)	18	0.7 (0.3, 2.0)	5
		2012	1.5 (1.0, 2.4)	22	1.6 (1.1, 2.6)	21
		2013	0.4 (0.2, 0.9)	9	1.3 (0.6, 3.5)	6
Cape Verde shearwater	Brazilian Current	2010	0.5 (0.2, 1.6)	4	0.2 (0.1, 0.6)	5
		2011	0.4 (0.2, 1.7)	4	0.6 (0.2, 2.0)	4

Table S14. Linear mixed models (LMMs) testing for sex, species and the size of the core area of wintering distribution effects on the Bayesian estimate of the standard ellipse area (SEAb) used as an approach to characterize the isotope niche widths (INW) of the three *Calonectris* species. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments of each model in comparison with the best model; AICc$_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model, and the models with ΔAICc < 2, are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parenthesis) with adjusted SE obtained after performing model averaging between the best-supported models with ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. All evaluated models included non-breeding area and year as random effects.

INW			
(a) Fixed factors structure	**AICc**	**ΔAICc**	**AICc$_{weight}$**
Constant	**91.7**	**0.0**	**0.405**
Species	**92.9**	**1.2**	**0.227**
Core area	94.0	2.3	0.130
Sex	94.4	2.7	0.106
Core area + Species	96.0	4.3	0.047
Sex + Species	96.1	4.3	0.047
Core area + Sex	97.0	5.2	0.030
Core area + Sex + Species	99.6	7.8	0.008
Sex + Species + Sex:Species	103.7	11.9	0.001
Core area + Sex + Species + Sex:Species	108.0	16.3	0.000
(b) Fixed effects		**Estimates**	
Core area		1.0 (0.7, 1.4)	
Cory's shearwater		0.8 (0.1, 1.4)	
Scopoli's shearwater		1.5 (0.9, 2.0)	
Cape Verde shearwater		0.4 (-0.6, 1.4)	
(c) Relative variance importance (%)			
Sex		0.1	
Species		0.4	
Core area		0.2	

Chapter 9

ANNEX

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ORIGINAL RESEARCH

Does sexual segregation occur during the nonbreeding period? A comparative analysis in spatial and feeding ecology of three *Calonectris* shearwaters

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Abstract

Sexual segregation (SS) is widespread among animal taxa, with males and females segregated in distribution, behavior, or feeding ecology but so far, most studies on birds have focused on the breeding period. Outside this period, the relevance of segregation and the potential drivers of its persistence remain elusive, especially in the marine environment, where animals can disperse over vast areas and are not easily observed. We evaluated the degree of SS in spatio-temporal distribution and phenology, at-sea behavior, and feeding ecology during the nonbreeding period among three closely related shearwaters: Scopoli's, Cory's, and Cape Verde shearwaters (*Calonectris diomedea*, *C. borealis*, and *C. edwardsii*, respectively). We tracked 179 birds (92 males and 87 females) from 2008 to 2013 using geolocation-immersion loggers and collected the 13th secondary remige (molted in winter) for stable isotope analyses as a proxy of trophic level and diet. The global nonbreeding distribution did not differ between sexes for the three species, but one specific nonbreeding area was visited only by males. Cory's shearwater males remained in areas closer to the colony in a larger proportion compared to females and returned earlier to the colony, probably to defend their nests. Males presented a slightly lower nocturnal flying activity and slightly (but consistently) higher isotopic values of δ^{13}C and δ^{15}N compared to females. These differences suggest subtle sexual differences in diet and a slightly higher trophic level in males, but the extent to which sexual dimorphism in bill size can determine them remains unclear. Our study showed that SS in ecological niche in seabirds can persist year-round consistently but at a different extent when comparing the breeding and nonbreeding periods. Based on our findings, we propose that SS in these seabird species might have its origin in an ecological specialization derived from the different roles of males and females during reproduction, rather than from social dominance during the nonbreeding period.

KEYWORDS
diet specialization, geolocation, nonbreeding distribution, seabird migration, sexual size dimorphism, stable isotope analyses

1 | INTRODUCTION

Sexual segregation (SS) is a widespread behavioral and ecological phenomenon in animal taxa (Rubin & Bleich, 2005). In many terrestrial and aquatic animal species, males and females differ in their spatio-temporal distribution, at-sea behavior, and feeding ecology (Catry, Phillips, & Croxall, 2005). SS emerges when males and females make different use of some suitable habitats or food resources, which may ultimately result in intersexual differences in fitness or survival rates, since sexes may be exposed to different conditions or threats (Harrison, Blount, Inger, Norris, & Bearhop, 2011; Marra & Holmes, 2001). Differences in mortality rate among sexes can lead to an imbalance in the sex ratio, with consequences at the population level and broad implications for population dynamics, species conservation, and wildlife management (Durell, Goss-Custard, & Clarke, 2001; Phillips, Silk, Croxall, Afanasyev, & Bennett, 2005).

Two broad hypotheses have been proposed to explain the general patterns of SS in animals. The social dominance hypothesis suggests that dominant individuals (usually males) tend to exclude subordinates (often females and immatures) from specific areas to access to high-quality food resources (Gauthreaux, 1978). The ecological specialization hypothesis proposes that habitat segregation arises from sex-specific preferences, tolerance to ecological factors, or specialization in reproductive roles (Carey, 1996; Ketterson & Nolan, 1983; Morton, 1990; Selander, 1966). Both hypotheses are not mutually exclusive, and their underlying mechanisms can co-occur and be both cause and consequence (Catry et al., 2005; González-Solís, Croxall, & Wood, 2000; Shine, 1989).

In birds, sexual differences in migration patterns could be explained by mechanisms related to either of these two general hypotheses, such as competition (related to the social dominance hypothesis) or body size and physiology (both related to the ecological specialization hypothesis; Cristol, Baker, & Carbone, 1999; Gauthreaux, 1982; Ketterson & Nolan, 1983; Myers, 1981). In general, dominant birds tend to remain sedentary and force subordinate individuals to move to areas farther from the breeding grounds to winter (Catry, Dias, Phillips, & Granadeiro, 2013; Gauthreaux, 1982; Pérez, Granadeiro, Dias, Alonso, & Catry, 2013). Furthermore, individuals with a larger body size and better individual physiology (i.e., better thermal tolerance or fasting endurance) would be able to withstand winter in areas closer to the breeding grounds (Ketterson & Nolan, 1976). The tendency of dominant birds to remain resident could also be explained by the arrival time hypothesis, which proposes the earlier arrival of one sex at the end of a migratory journey (related to the ecological specialization hypothesis). According to this hypothesis, the dominant sex tends to be more pressed to arrive earlier at the breeding grounds to gain advantage when competing for better territories or nest sites for breeding (rank advantage hypothesis; Morbey & Ydenberg, 2001) and/or favors more mating opportunities (mate opportunity hypothesis; Morbey & Ydenberg, 2001).

Another indirect mechanism favoring SS is the degree of sexual size dimorphism (SSD) of the species. SSD can contribute to social dominance, as the larger sex is usually the dominant one. Social dominance of one sex can lead to the spatial exclusion of the other at various spatial scales, ranging from subtle differences in microhabitat to disparate geographical distributions (Catry et al., 2005; Staniland, 2006). Nevertheless, SSD can also lead to ecological specialization, due to divergent nutritional and energetic requirements (Main & Coblentz, 1990; Newton, 2008; Ruckstuhl & Neuhaus, 2002), and/or to niche or dietary specialization. The latter occurs when males and females use similar foraging areas but specialize on different prey types due to the morphological differentiation in feeding or locomotion structures (Bearhop et al., 2006; Phillips, McGill, Dawson, & Bearhop, 2011).

Since ecological specialization may arise from differences in the roles of males and females during reproduction, sex-specific differences in spatio-temporal distribution and feeding ecology have been widely studied during the breeding period (Elliott, Gaston, & Crump, 2010; Stauss et al., 2012; Thaxter et al., 2009; Weimerskirch et al., 2009). However, studying behavioral and ecological sexual differences out of the breeding period, especially among migratory species, can be challenging due to sampling constraints and limited accessibility to individuals, particularly in the marine environment. As a result, the relevance of SS and the mechanisms of its persistence over the nonbreeding period remain elusive (Alves et al., 2013; Alves et al., 2013; Croxall, Silk, Phillips, Afanasyev, & Briggs, 2005; Müller, Massa, Phillips, & Dell, 2014).

Our capacity to study the spatial and feeding ecology of migratory species during the nonbreeding period has improved considerably in the last decades due to the possibility to combine the deployment of light-level geolocation devices (geolocators hereafter) and stable isotope analysis (SIA). Geolocators can inform us about the year-round phenology, movements, distribution, and at-sea activity patterns (in those cases where loggers are also equipped with an immersion sensor) of a given species. SIA can provide us with information on the feeding and spatial ecology when species feed on isotopically different prey or in areas with distinct isotopic baseline values (Ramos & González-Solís, 2012). Feathers are metabolically inert after growing and, therefore, their isotopic values reflect the food assimilated by birds during their synthesis (Hobson & Clark, 1992; Ramos & González-Solís, 2012). Thus, by analyzing feathers molted during the nonbreeding period, we can infer the feeding ecology of birds during such an otherwise inaccessible life stage.

Calonectris shearwaters are wide-ranging species, performing long-distance migrations across ocean basins after the breeding period and spreading over diverse nonbreeding areas (González-Solís, Croxall, Oro, & Ruiz, 2007; Thibault, Bretagnol, & Rabouam, 1997), thus exposing the individuals to variable environments that can lead to SS in foraging strategies in different ways (Åkesson & Weimerskirch, 2014; Bearhop et al., 2006; Ceia et al., 2012; Phillips, Bearhop, McGill, & Dawson, 2009; Figure 1). These species are relatively well-studied during the breeding period, and many studies have been done with respect to their SS (Alonso et al., 2014; Werner, Paiva, & Ramos, 2014; Cianchetti-Benedetti, Catoni, Kato, Massa, & Quillfeldt, 2017; Matsumoto, Yamamoto, Yamamoto, Zavalaga, & Yoda, 2017; Navarro, Kaliontzopoulou, & González-Solís, 2009; Paiva, Pereira, Ceia, & Ramos, 2017; Ramos, Granadeiro, Phillips, & Catry, 2009a; Ramos, González-Solís, et al., 2009b). In these species, SS in foraging behavior and feeding ecology may be shaped by annual and seasonal prey availability (Paiva et al., 2017), differences in reproduction duties over the breeding period (Werner et al., 2014; Ramos, González-Solís, et al., 2009b), and/or could be related to SSD between sexes (Alonso et al., 2014; Cianchetti-Benedetti et al., 2017). However, while many of these studies did find evidence of sexual differences in foraging and feeding ecology during the breeding period (Alonso et al., 2014; Werner et al., 2014; Cianchetti-Benedetti et al., 2017; Matsumoto et al., 2017; Paiva et al., 2017; Ramos, González-Solís, et al., 2009b), many others did not find any clear difference (Navarro, González-Solís, & Viscor, 2007; Navarro et al., 2009; Ramos, Granadeiro, et al., 2009a). Nonetheless, the degree to which SS in foraging performance continues out of the breeding period is still poorly known in these species (Müller et al., 2014).

In this study, we evaluated the degree of SS in spatial and feeding ecology during the nonbreeding period of three closely related shearwaters: the Scopoli's, Cory's, and Cape Verde shearwaters (*Calonectris diomedea*, *C. borealis*, and *C. edwardsii*, respectively). In general, we expect that SS in spatial and feeding ecology occurring during the breeding period will not persist during the nonbreeding period, since during this period, seabirds do not have different reproductive roles, are not constrained to return to their nests, and can range for many thousands of kilometers to winter in the most productive areas of the ocean (Bost et al., 2009; Egevang et al., 2010; Shaffer et al., 2006), reducing between-sex competition and partitioning of food resources (Phillips et al., 2011). Specifically, we aim to test the following three hypotheses: (a) As the larger size of males has been related to a greater involvement in nest defense at the beginning of the breeding period (Werner et al., 2014; Hedd, Montevecchi, Phillips, & Fifield, 2014), we expect males to return to the breeding colonies earlier than females, in accordance with the arrival time hypothesis. (b) Since during the nonbreeding period foraging ranges are not constrained, and shearwaters disperse over wider areas to winter (Shaffer et al., 2006; González-Solís et al., 2007), we expect that both sexes would share the same nonbreeding areas, and males would not exclude females from areas with high-quality food resources. (c) Previous studies found differences between sexes in the bill shape and size to be poor predictors of the way males and females (of Cory's shearwaters) exploit the marine environment (Navarro et al., 2009; Ramos, González-Solís, et al., 2009b). Moreover, between-sex competition for resources is less intense during the nonbreeding period (González-Solís et al., 2000). Thus, we expect that males and females would not present differences in their feeding ecology during this period and would feed on similar prey items. Predictions (b) and (c) would refute the social dominance hypothesis for the nonbreeding period, whereas prediction (a) would support the arrival time hypothesis for migratory seabirds. To this end, we evaluated sexual differences during the nonbreeding period of Scopoli's, Cory's, and Cape Verde shearwaters in (a) spatio-temporal distribution (inferred through geolocation data), (b) at-sea activity behavior (inferred through immersion data), and (c) feeding ecology (inferred through SIA on one specific feather known to be molted in the winter quarters). Finally, as greater SSD can lead to greater SS (Abouheif & Fairbairn, 1997; Fairbairn, 1997), we also determined the degree of SSD of each species and explored the potential influence of bill size on its feeding ecology.

FIGURE 1 Breeding pair of Cory's shearwaters at Montaña Clara colony, Canary Islands photographed inside their nest in 2008. Photograph by Jacob González-Solís

2 | MATERIALS AND METHODS

2.1 | Study species and sampling protocol

Scopoli's shearwater is an endemic breeding species in the Mediterranean Basin, ranging from the Iberian coast to the Adriatic and Aegean Seas (Gómez-Díaz & González-Solís, 2007). Cory's shearwaters breed on several islands in the northeast Atlantic Ocean and in a few small colonies in the western Mediterranean Sea (Gómez-Díaz, González-Solís, & Peinado, 2009). The Cape Verde shearwater is an endemic breeding species in the Cape Verde Islands (Hazevoet, 1995). Scopoli's and Cory's shearwaters are classified as “Least concern” according to the Red List criteria of the International Union for the Conservation of Nature (IUCN; BirdLife International, 2018), whereas the Cape Verde shearwater is listed as “Near Threatened” due to its restricted breeding distribution (Hazevoet, 2003).

Calonectris shearwaters breed mainly on islands and islets, nesting in burrows and crevices. Breeding females lay a single egg per season, and both parents share similar incubation and chick-rearing duties throughout the breeding season (Granadeiro, Dias, Rebelo, Santos, & Catry, 2006; Thibault et al., 1997). All three species show slight sexual dimorphism in body size, with females being slightly smaller than males in wing length, tarsus length, and bill dimensions and having a less robust shape (Granadeiro, 1993; Massa & Lo Valvo, 1986; Navarro et al., 2009). The breeding phenology of the three species is similar in time: Birds return to the colony from the nonbreeding areas in late February/early March, the laying period begins in the second half of May, and chicks start hatching in mid-July. Fledglings usually leave the colonies from mid-October to early November (Granadeiro, 1999; Hazevoet, 1995; Thibault et al., 1997). All three species spend the nonbreeding period in the Atlantic Ocean, mainly in the South Atlantic in areas associated with major upwellings (such as the Benguela and

TABLE 1 Summary characteristics of the study colonies and the number of males and females of Scopoli's, Cory's, and Cape Verde shearwaters sampled and tracked in the study period

					Sample size		Tracks	
Species	**Breeding colony**	**Longitude (°)**	**Latitude (°)**	**Sampling years**	**Males**	**Females**	**Males**	**Females**
Scopoli's shearwater	Pantaleu islet (Balearic Islands)	2.35	39.57	2009–2013	22	22	35	35
Cory's shearwater	Vila islet (Azores Islands)	−25.17	36.94	2010–2012	12	6	16	9
	Montaña Clara (Canary Islands)	−13.53	29.29	2011–2013	9	11	12	16
	Veneguera (Canary Islands)	−15.78	27.84	2008–2013	44	38	92	76
Cape Verde shearwater	Curral Velho islet (Cape Verde)	−22.78	15.96	2008–2011	5	10	10	14

Angola Currents and Brazil Current), and the Canary Current. However, Cory's shearwater can present a broader distribution, with some birds wintering in the North Atlantic and in the southwestern Indian Ocean (González-Solís et al., 2007; Müller et al., 2014; Petry, Bugoni, & Silva Fonseca, 2000).

In up to five breeding colonies (Table 1), adult birds were captured in their burrows during the breeding period, ringed, and tagged with geolocators. During the subsequent breeding period, we recaptured the birds, retrieved the geolocator, cut the 13th secondary remige (S13 hereafter) for SIA, and we equipped the birds with a new geolocator. During one of the recaptures, we also took a blood sample for molecular sexing and biometric measurements for SSD assessment.

2.2 | Molecular sexing

All individuals in the study were molecularly sexed. DNA was extracted from ethanol-preserved whole blood using a Real Pure genomic DNA extraction kit (Durviz, Spain) following the manufacturer's instructions. Polymerase chain reactions (PCRs) were performed following the method of Fridolfsson and Ellegren (1999), previously used to identify the sex in a large variety of Procellariiform species. Sex determination was based on the detection of a female-specific locus, CHD1-W.

2.3 | Biometric measurements and sexual size dimorphism

We measured five biometric variables on 44, 54, and 16 individuals of Scopoli's, Cory's, and Cape Verde shearwaters, respectively: tarsus length, culmen length, maximum head length (head plus bill length), bill depth at the base, and bill depth at the nostrils. Measurements were taken using digital calipers (±0.01 mm). We assessed the SSD for each biometric measurement and for each study species. SSD index (SSI hereafter) was calculated as:

$$\mathrm{SSI} = \left(\frac{\text{male's average} - \text{female's average}}{(\text{male's average} + \text{female's average}) \times 0.5} \right) \times 100.$$

This index is recommended due to its simplicity and because it maintains symmetry around a neutral zero, indicating monomorphy (Storer, 1966). Furthermore, it complies with the convention of positive values in cases where males are the larger sex and negative values in cases where females are the larger ones (Greenwood, 2003). To check the influence of bill SSI on the feeding ecology of the shearwaters, we pooled all individuals measured (N = 144) and performed a principal component analysis (PCA) on culmen length, maximum head length, bill depth at the base, and bill depth at the nostrils per each individual. Axis 1 explained a high proportion (92%) of the total variance (Table S1). Therefore, the first principal component scores (scores on axis 1, hereafter referred to as PC1 scores) were used as a proxy of bill size in further statistical analyses (Rising & Somers, 1989).

2.4 | Geolocation light data

To evaluate whether adult males and females of each species differ spatially in their distribution and/or phenology during the nonbreeding period, we equipped several adult birds of each species with geolocators. The geolocator was attached to a PVC ring with a cable tie, and the ring was put on the leg of the bird. The weight of the geolocators varied from 1.8 g to 4.5 g, depending on the model (models Mk4, Mk9, Mk13, Mk14, Mk18-H, and Mk19 from the British Antarctic Survey and Mk3005 from Biotrack), corresponding to <1.2% of bird body mass, which is known to have negligible effects on the birds (Carey, 2009; Igual et al., 2005). Overall, we collected information from 70, 221, and 24 geolocators from Scopoli's, Cory's, and Cape Verde shearwaters, respectively, deployed on 182 individuals (Table 1).

Geolocators are devices that record and store ambient light information. The intensity of light is measured every 60 s, and the maximum reading is recorded in 5- or 10-min intervals, depending on the model. Sunset and sunrise times are estimated from thresholds in light curves and are converted into latitudes and longitudes since every location on the planet has a unique combination of time of sunrise and photoperiod in each hemisphere (Hill, 1994), except during the equinoxes. Latitude was derived from day length and longitude from the time of local midday with respect to Greenwich Mean Time. Thus, we assessed

two positions of the bird per day with an average accuracy of approximately 186 ± 114 km (Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004). Light data were analyzed visually for every geolocator, using TransEdit and Bird Tracker softwares (British Antarctic Survey, UK), and unrealistic positions were filtered by: (a) removing data during equinoxes due to the inaccuracy of latitude estimation (ca. 20 days before and after the equinoxes); and (b) removing the positions from light curves with obvious interference during the times of sunset or sunrise. We set to 20 the threshold light level considered as the transition between day and night in order to avoid interferences of light during the night and darkness during the day. Before obtaining the trajectory of each bird, sun elevation angles (ranged for −6° to −3°) were calculated based on known positions obtained during a calibration period (approximately 1 week) carried out before the deployments and after recoveries at the breeding colonies. Finally, we smoothed the filtered data twice by interpolating intermediate fixes between successive locations as recommended by Phillips et al. (2004).

To assign each bird (and year) to a single nonbreeding area, we first computed the utilization distribution kernel (KUD hereafter) with previously filtered geolocation data using the function "kernelUD" (R package adehabitat v.1.8.71, Calenge, 2006). We used a bandwidth equivalent to 186 km (~2°, depending on latitude) to account for the average reported error in geolocation (Phillips et al., 2004). Later, we extracted the 50% density contour of the KUD and determined the centroid, using the function "gCentroid" from the R package rgeos (Bivand & Rundel, 2017). We performed a chi-square test per colony based on the proportion of each sex in each nonbreeding area to determine whether a sexual preference for the use of specific nonbreeding areas existed. In case the 50% density contour of the KUD of a bird was comprised by more than one polygon, the centroid considered for assigning a main nonbreeding area was the one corresponding to the polygon where the bird spent the highest number of days.

In order to determine differences between sexes in the size of the areas used during winter, we first computed KUD using filtered positions for each nonbreeding area and year using a Lambert azimuthal equal-area projection centered in the centroid of locations to allow area comparability. Next, we calculated the size of the 95% and 50% KUD contours (function "gArea," package rgeos, Bivand & Rundel, 2017), which were considered to represent the general use and core areas of the wintering distribution, respectively. Lastly, we quantified the amount of overlap between females and males in the general use and core areas of wintering distribution using the "kerneloverlap" function and "HR" method of the adehabitatHR package (Calenge, 2006).

To infer the migratory phenology of our study birds, the filtered positions were inspected visually using Locator software (British Antarctic Survey, UK). Departure dates (from colonies and nonbreeding areas) were defined as the first position outside the cluster of positions of the 10 previous days, when birds shifted behavior and began a rapid directional flight moving away from that cluster. Similarly, arrival dates were defined as the first position of the birds within the cluster of the positions recorded during the days after a rapid directional flight. During the equinoxes, the departure and arrival dates were determined based on the birds' longitude changes (not affected by the equinoxes) as, in most cases, the migratory movement was mainly longitudinal (e.g., Scopoli's shearwater departure from the colony westward toward the Atlantic). In the case of arrival at the breeding colonies occurring during the equinox, we defined the arrival date as the first night the bird spent all night dry (resting at the colony).

2.5 | At-sea activity data

The geolocator models used also incorporate a saltwater switch that measures conductivity from immersion in saltwater every 3 s, and combines this information at every 10-min interval. Given the sampling interval (3 s), the values recorded at the end of each 10-min period range from 0 (10-min period in dry mode = no conductivity detected) to 200 (10-min period in wet mode). These data can be used to infer the behavior of the birds during the nonbreeding season: Complete dryness (0) means that the birds are flying; complete wetness (200) means that the birds are resting (sitting on the sea surface) or diving; and alternate modes between dry and wet (1–199) mean that birds are alternating flying and resting, or could also suggest foraging behavior (Lecomte et al., 2010; Mattern, Masello, Ellenberg, & Quillfeldt, 2015).

To assess whether males and females behave differently at sea during the nonbreeding period, we calculated the night flight index (NFI; Dias, Granadeiro, & Catry, 2012b) of every bird for the period spent in the main nonbreeding area. The ratio of nocturnal/diurnal activity may be associated with prey targeted and thus can provide information about feeding strategies (Dias et al., 2016; Regular, Davoren, Hedd, & Montevecchi, 2010; Spear, Ainley, & Walker, 2007). NFI represents the difference between the proportion of time spent flying during darkness and the proportion of time spent flying during daylight, divided by the highest of these two values, and it varies between −1 (flight activity exclusively during daylight) and 1 (flight activity exclusively during darkness). Moonlight intensity affects activity patterns of shearwaters (Dias, Granadeiro, & Catry, 2012a; Yamamoto et al., 2008). Thus, to control for the influence of moonlight intensity on NFI values, we selected data for an entire lunar cycle (28 days) within the nonbreeding period per individual and year, calculated the NFI for every day of this lunar cycle, and, finally, calculated the mean NFI value per individual and year.

2.6 | Stable isotope analyses

Stable isotope analyse (SIA) of feathers can be used to study the feeding ecology of seabirds (Hobson, 1999). Feathers become metabolically (and isotopically) inert once fully formed and maintain the isotopic composition of the period and area when they were synthesized, independently of the sampling time (Hobson & Norris, 2008). Knowing the molting patterns of the study species is crucial for SIA, since it allows us to choose which feather to analyze, depending on the period of interest. The molting patterns of Scopoli's and Cory's shearwaters are relatively well known (Alonso, Matias, Granadeiro, & Catry, 2009; Camphuysen & Van Der Meer, 2001; Ramos, Militão, González-Solís, & Ruiz, 2009c), and they are rather similar between these species. Thus, we assumed it would also be similar for the Cape Verde shearwater. We collected the S13 remige for SIA as this feather is known to be molted at the middle to end of the nonbreeding period in Scopoli's and Cory's shearwaters (since the molt of secondary remiges is asynchronous, and the foci of 12th–16th secondary remiges are the last to be molted; Ramos, Militão, et al., 2009c). In general, $\delta^{15}N$ increases by 3%–5‰ with each trophic level (DeNiro & Epstein, 1981). $\delta^{13}C$ also increases with trophic level, although in a smaller proportion (approximately 1‰; Rau, Ainley, Bengtson, Torres, & Hopkins, 1992). The main causes of variations in $\delta^{13}C$ are differences in photosynthetic biochemistry within and among marine primary producer communities (Farquhar, Ehleringer, & Hubick, 1989; Robinson, 2001). Hence, in marine ecosystems, we can infer the origin of food sources from the $\delta^{13}C$ gradients that exist between water masses, gradients between inshore/offshore waters, and benthic/pelagic habitats, while $\delta^{15}N$ values can be used to assess the trophic positions of consumers (Cherel & Hobson, 2007; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007).

Once at the laboratory, feathers were washed in a 0.25 M NaOH solution, thoroughly rinsed twice in distilled water to remove any surface contamination, and dried in an oven at 40°C to constant mass. Afterward, we freeze-milled all feathers to fine powder in a cryogenic impact grinder (Freeser/mill Spex Certiprep 6750; Spex) operating at liquid nitrogen temperature. We weighed subsamples of 0.30 to 0.32 mg of feather powder and placed them in tin capsules. These samples were oxidized in a Flash EA1112 and TC/EA coupled to a stable isotope mass spectrometer Delta C through a ConFLO III interface (Thermo Finnigan), and, finally, $\delta^{13}C$ and $\delta^{15}N$ values were determined. Isotope ratios (R) of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ are expressed conventionally in δ units as parts per thousand (‰) according to the following equation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right),$$

where X (‰) is ^{13}C or ^{15}N and R are the corresponding ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$ related to the standard values. The international standards for SIA are Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N_2 (AIR) for nitrogen. The SIAs were performed at the Serveis Científico-Tècnics of the University of Barcelona (Spain), where international standards (IAEA CH_7, IAEA CH_6, and USGS 40 for C and IAEA N_1, IAEA N_2, IAEA NO_3, and USGS 40 for N) are applied and two standard material samples are inserted every 12 feather samples to calibrate the system and compensate for any drift over time (Böhlke, Mroczkowski, & Coplen, 2003; Böhlke & Coplen, 1995; Coplen et al., 2006; Qi, Coplen, Geilmann, Brand, & Böhlke, 2003; Table S2). The overall measurement error is on average of 0.2‰ for carbon isotopes and 0.3‰ for nitrogen isotopes. All the samples were homogenized by milling them to a fine powder, so we believe that was not necessary to run duplicates. The entire feather analysis methodology was conducted following the "principle of identical treatment" (Bond & Hobson, 2012).

Isotopic data were used to characterize the isotopic niche widths (INW) of each sex through Bayesian statistical ellipses (stable isotope Bayesian ellipses in R—SIBER). We compared INW using a Bayesian estimate of the standard ellipse area (SEAb) to test the probability of a group ellipse of one of the sexes being smaller than the other (Jackson, Inger, Parnell, & Bearhop, 2011). To have a correct estimation of the ellipses, we only considered those nonbreeding areas and years used for a minimum of four birds per sex. Despite the small sample size, it is known that the Bayesian implementation of the ellipse area measurement is less affected by sample size than the convex hull, SEA, and SEAc (Jackson et al., 2011). In addition, using the Bayesian estimation allowed us to provide uncertainty measures (95% credible intervals) around point estimates for the ellipse areas.

2.7 | Statistical analyses

We performed linear mixed-effects models (LMMs) to check for sexual differences in the following spatial, phenological, behavioral, and feeding ecological features:

1. Phenological parameters of the migration (represented as day of the year): departure date from the breeding colony (postbreeding migration), days in transit to the nonbreeding areas, total duration of the nonbreeding period, days in the nonbreeding areas, onset of the prebreeding migration, and days in transit returning to the colony and arrival at the breeding colony. These parameters can only be calculated for migratory birds, so we excluded those birds that remain year-round near the breeding grounds. Nevertheless, we also tested for differences in the date of arrival at the breeding colony between migratory and nonmigratory males of Cory's shearwater and between nonmigratory males and females of Cory's shearwater;
2. Maximum distance traveled from the colony to the centroid of the wintering distribution;
3. Mean size of the core areas of the wintering distribution;
4. NFI values;
5. INW estimated for each nonbreeding area, as indicated by the SEAb values;
6. Values of $\delta^{13}C$ and $\delta^{15}N$ assessed on S13 remiges.

Regarding the structure of the models, we always included sex and species as fixed effects. In the models testing for differences in the arrival date at the breeding colony between migratory and nonmigratory Cory's shearwater males, we included migratory behavior (migratory or nonmigratory) and nonbreeding areas as fixed effects. In the models of $\delta^{13}C$ and $\delta^{15}N$, we also included bill size (PC1 scores of bill measurements) as a covariate when testing the effect of the sexual dimorphism on trophic ecology. In the models considering INW, we also included the size of the core area of the wintering distribution within nonbreeding areas as a covariate. Except when modeling INW, bird identity and year were included as random effects to avoid pseudoreplication and nonindependent measurements. When modeling INW, we only included nonbreeding area as a random term, since the INW is calculated by each sex and it is not an individual estimate. When determining the factors affecting migration phenology and the values of δ^{13}C and δ^{15}N, we also included nonbreeding area as a random term, as well as bird identity and year. Lastly, in the models testing for differences in arrival date at the breeding colony between migratory and nonmigratory males of Cory's shearwater, we included the breeding colony as a random term.

All statistical analyses were performed using R software (version 3.2.5, R Development Core Team, 2010). LMMs were conducted with the function “lmer” (R package lme4, Bates, Mächler, Bolker, & Walker, 2015). To ensure accomplishment of normality and homoscedasticity, we visually inspected Q–Q plots scatter plots of residuals versus fitted values. We created a set of competing models (the first as the full model, including all fixed factors and double interactions) and selected the most parsimonious models, that is, the models that better explain our data using fewer parameters, based on the Akaike's information criterion corrected (AICc) for small sample sizes using the function “dredge” (R package MuMIn, Kamil, 2017). According to the AICc weight (Burnham & Anderson, 2002), we removed nonsignificant terms from our models. When ΔAICc was <2 between our best models, these models explained the data equally well, thus we could not determine which one was the most parsimonious (Burnham & Anderson, 2002). To address this issue, we performed model averaging using the function “model.avg” (R package MuMIn, Kamil, 2017) of those models with ΔAICc < 2 to obtain estimates for our variables. Finally, we performed post hoc comparisons by calculating the differences between the least-squares means within fixed factors of our best models using the function “difflsmeans” (R package lmerTest, Kuznetsova, Brockhoff, & Christensen, 2015). Whenever multiple comparisons with the same variables were performed, we applied Bonferroni corrections to calculate the correct statistical significance according to the numbers of tests performed.

3 | RESULTS

3.1 | Biometric measurements

Sexual size dimorphism index was generally low. Tarsus of Cory's shearwater presented the lowest value (3.4%), whereas bill depth at the nostrils in Scopoli's shearwater showed the highest value (13.4%). Males were, on average, larger than females for the three species, although values of standard deviations overlapped in some extent (i.e., larger females overlapped in size with smaller males). For the three species, differences were more pronounced in bill measurements than in tarsus or maximum head lengths. Scopoli's shearwaters showed the highest SSI among the study species (Tables S3 and S4).

3.2 | Spatial ecology

3.2.1 | Migratory patterns

When testing for sex and species effects on eight migratory parameters, the most parsimonious LMMs always retained species as explanatory factors, and most models also retained sex (Table S5). No sexual differences were found in the maximum distance traveled from the colony to the centroids of the nonbreeding areas or in the number of days in transit to the nonbreeding areas (Tables S5 and S6). For the rest of variables describing migratory patterns, the two best models explained our data equally well (ΔAICc < 2) and, thus, we performed model averaging between them. Males left the colonies in autumn 4 days earlier, on average, than females. The total duration of the nonbreeding period (from departure and until the return to the breeding colony), as well as the number of days in the main nonbreeding areas, was greater for males than for females. Males started the prebreeding migration approximately 1 day earlier than females and arrived about 3 days earlier at the breeding grounds, spending fewer days in transit when returning to the colony (Table S5).

Since some Cory's shearwater individuals from Vila and Veneguera did not migrate and remained in areas close to their colonies, we tested whether the return date to the colony differed between nonmigratory and migratory birds. Most parsimonious LMM retained the migratory behavior, but did not retain nonbreeding areas as an explanatory factor. Nonmigratory males arrived about 23 days earlier at the breeding colonies when compared to migratory males. The random effect bird identity explained a higher proportion of the variance not explained by fixed factors than did year or breeding colony factors (Table 2).

Some male and female Cory's shearwaters from Veneguera did not migrate and remained in the Canary Current, near the colony. We tested whether sex influenced the date of arrival at the breeding colony in these nonmigratory birds. The most parsimonious LMM retained sex, and nonmigratory males returned to the colony about 5 days earlier than nonmigratory females (Table 3).

3.2.2 | Wintering distribution

Scopoli's shearwaters wintered in three main areas: the Canary Current (16 males, 12 females), the Guinea and Equatorial Currents (considered as a single area based on their geographical proximity; 7 males, 15 females), and the Angola and Benguela Currents (merged due to geographical proximity and uniformity of stable isotope values of the S13 of the individuals using this area (*t* test: δ^{15}N $t_{(16.807)} = -1.1571$ $p = 0.263$; δ^{13}C: $t_{(17.270)} = 1.3909$ $p = 0.182$; 12 males, 8 females). No difference was found in the use of the nonbreeding areas by males and females ($\chi^2 = 4.3$, $df = 3$, $p = 0.230$). For Cory's shearwater, we identified up to six nonbreeding areas: the North Atlantic area (7 males, 0 females), the South Atlantic area (6 males, 4 females), Canary Current (14 males, 10 females), the Angola and Benguela Currents (merged due to geographical

TABLE 2 Linear mixed model testing for potential effects of migratory behavior and nonbreeding area on the arrival date at the breeding colony of male Cory's shearwaters. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: Akaike's information criterion corrected; ΔAICc: AICc increments of each model in comparison with the best model; $AICc_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model is shown in bold. (b) Mean estimates (and 95% confidence intervals in parentheses) of the fixed effects. (c) Variance (±*SD*) and random variance explained (calculated as the percentage of the variance of each random effect divided by the total variance explained by all random effects) by the random effects. All evaluated models included bird identity, year, and breeding colony as random effects

Date of arrival at the breeding colony of migratory and nonmigratory males of Cory's shearwater			
(a) Fixed factors structure	**AICc**	**ΔAICc**	**$AICc_{weight}$**
Migratory	**949.5**	**0.0**	**0.702**
Nonbreeding area	952.6	3.1	0.149
Migratory + Nonbreeding area	952.6	3.1	0.149
Constant	972.0	22.4	0.000
(b) Fixed effects	**Estimates**		
Migratory males	68.3 (57.6, 79.9)		
Nonmigratory males	46.4 (33.1, 59.1)		
(c) Random Effects	**Variance ± *SD***		**Random variance explained (%)**
Individual	98.1 ± 9.9		32.7
Year	12.4 ± 3.5		4.1
Colony	46.4 ± 6.8		15.5
Residual	143.1 ± 12.0		47.7

TABLE 3 Linear mixed model testing for potential effects of sex on the arrival date at the breeding colony of the nonmigratory Cory's shearwaters from Veneguera. (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: Akaike's information criterion corrected; ΔAICc: AICc increments of each model in comparison with the best model; $AICc_{weight}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious model is shown in bold. (b) Mean estimates (and 95% confidence intervals in parentheses) of the fixed effects. (c) Variance (±*SD*) and random variance explained (calculated as the percentage of the variance of each random effect divided by the total variance explained by all random effects) by the random effects. All evaluated models included bird identity and year as random effects

Date of arrival to the breeding colony of nonmigratory Cory's shearwater			
(a) Fixed factors structure	**AICc**	**ΔAICc**	**$AICc_{weight}$**
Sex	**183.7**	**0.0**	**0.837**
Constant	187.0	3.3	0.163
(b) Fixed effects	**Estimates**		
Males	39.6 (26.5, 52.7)		
Females	44.6 (28.6, 60.5)		
(c) Random Effects	**Variance ± *SD***		**Random variance explained (%)**
Individual	18.8 ± 4.3		5.5
Year	52.7 ± 7.3		15.4
Residual	271.6 ± 16.5		79.2

proximity and uniformity of stable isotope values of the S13 of the individuals using this area (*t* test: $\delta^{15}N$ $t_{(3.187)} = 0.5719$ $p = 0.605$; $\delta^{13}C$: $t_{(3.048)} = 0.6692$ $p = 0.551$; 78 males, 59 females), the Agulhas Current (9 males, 14 females), and the Brazil Current (2 males, 12 females). We found that male and female Cory's shearwaters did not exploit their nonbreeding areas in a similar manner ($\chi^2 = 17.7$, $df = 5$, $p = 0.003$). More specifically, no female from Vila islet (Azores) wintered in the Benguela Current or the North Atlantic, while no male from this colony wintered in the Agulhas Current ($\chi^2 = 19.2$, $df = 4$, $p < 0.001$). Moreover, no female from Montaña Clara (Canary Is.) wintered in the Canary Current or the South Atlantic, while no males wintered in the Agulhas and Brazil Currents (Table S7; $\chi^2 = 9.7$, $df = 4$, $p = 0.052$). All Cape Verde shearwater individuals wintered in the Brazil Current throughout the study period (10 males, 14 females; Figure 2).

Regarding the size of the core areas of the wintering distribution, most parsimonious LMM retained sex as explanatory factor (Table S9). In general, females used a greater core area than males ($mean_{males} = 618{,}646$ km^2 [365,730–871,560], $mean_{females} = 806{,}545$ km^2 [553,630–1,059,460]). For most years and nonbreeding areas, females of Scopoli's and Cory's shearwaters globally used a greater core area than males within each nonbreeding area. In contrast, males of Cape Verde shearwater showed larger core areas in the Brazil Current during the two years studied (Table S8). Finally, both sexes showed a high degree of overlap in their general use areas (95% Kernel density contours) and in the core areas (50% Kernel density contours) for most nonbreeding areas and years (Table S10).

3.2.3 | At-sea behavior

Night flight index revealed differences among sexes and species. Our model suggested that the females of Scopoli's and Cape Verde shearwaters tended to be more active during the night than males. Cory's shearwaters presented the opposite pattern, and, overall, this species was more active at night than the other two (Table S11).

3.3 | Trophic ecology

3.3.1 | Stable isotope analysis

Overall, the S13 of the males of the three species showed slightly higher values of $\delta^{13}C$ ($\text{mean estimates}_{males} = -15.6$ [−16.2, −15.1]) and $\delta^{15}N$ ($\text{mean estimates}_{males} = 14.0$ [12.8, 15.3]) than in females ($\text{mean estimates}_{females} = -15.8$ [−16.3, −15.3]) and 13.5 [12.3, 14.7] for $\delta^{13}C$ and $\delta^{15}N$ values, respectively; Figure 3 and Table 4).

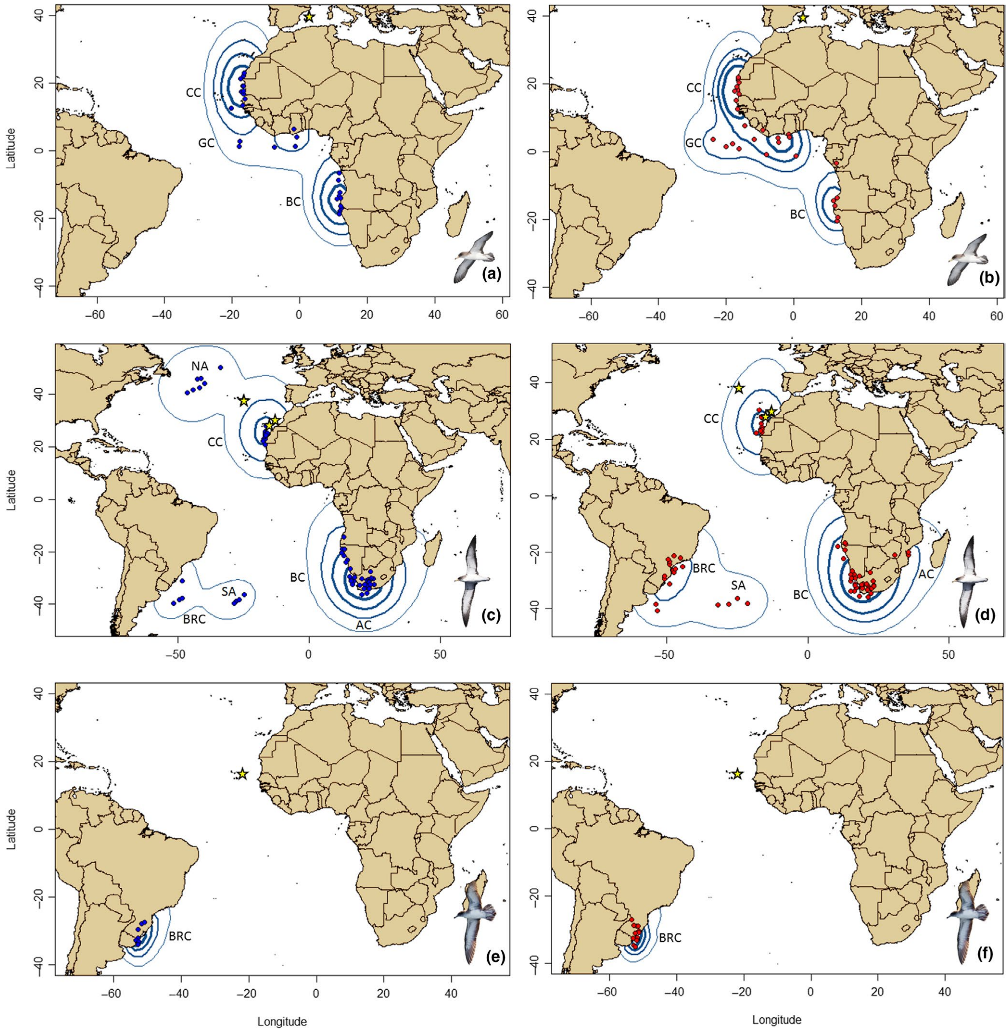

FIGURE 2 Nonbreeding destinations of males (left, in blue) and females (right, in red) of Scopoli's (a, b), Cory's (c, d), and Cape Verde (e, f) shearwaters: AC = Agulhas Current, BC = Benguela Current, BRC = Brazil Current, CC = Canary Current, GC = Guinea Current, NA = North Atlantic, and SA = South Atlantic. Dots represent the centroid of the nonbreeding position of each individual and year (calculated as averaged coordinates of every 50% UD kernel). UD kernel (25%, 50%, 75%, and 95%, from thicker to lighter blue line contours, respectively) for each sex, and species are also depicted. Yellow stars represent the position of the breeding colonies. Note that, although filters were applied to geolocator data, a percentage of locations occurs on land because of the still relevant influence of the equinoxes. As a result, some individual centroids are on land, although we actually know shearwaters rarely travel inland. Note also that locations over the sea are subject to the same error rate as those on land, although, in this case, it is difficult to recognize

The best models for explaining differences in $\delta^{13}C$ and $\delta^{15}N$ values included sex, species, their interaction, and bill size. Although all variables were retained in the best models (with exception of the interaction between sex and bill size), the relative importance and significance of sex (1.0) and species (1.0) were higher when comparing with bill size (0.3 and 0.4 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively;

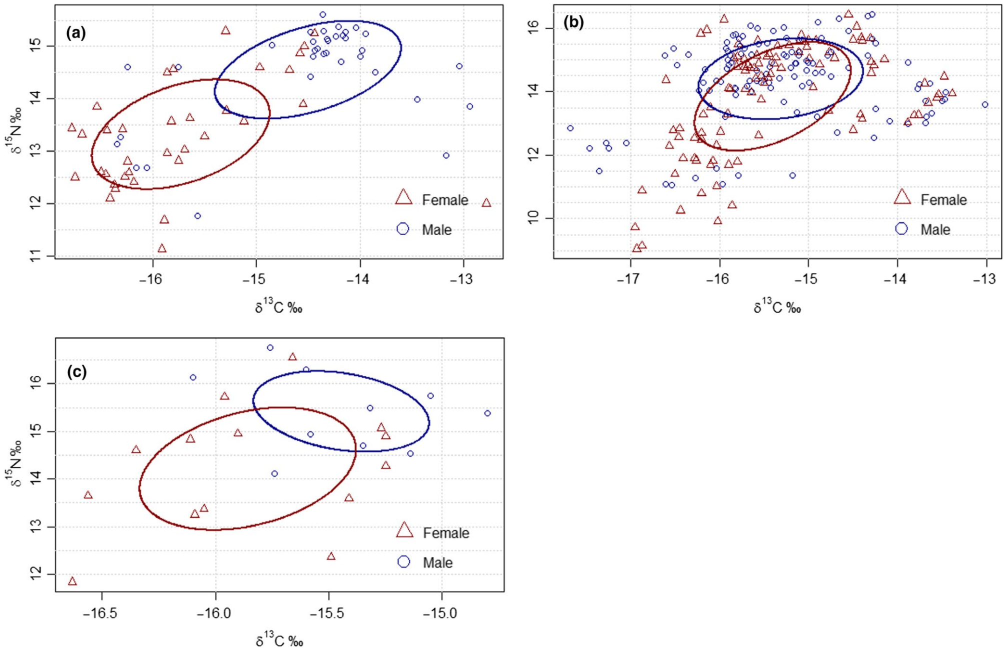

FIGURE 3 Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ of the 13th secondary remiges (S13) of Scopoli's (a), Cory's (b), and Cape Verde (c) shearwaters for all the study years (2008–2013). The area of the standard ellipses (SEAc) used to compare isotopic niches are represented by solid lines (ellipses; see Jackson et al., 2011). Males are denoted in blue and females in red

Table 4). Thus, we performed separate pairwise comparisons, and despite the lack of statistical significance for all the three species, isotopic values were, in general, slightly higher in males (mean estimates = 0.6 [0.3, 0.9], $p < 0.001$ and mean estimates = 0.9 [0.5, 1.4], $p < 0.001$ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively). The mean values of $\delta^{13}C$ (mean estimates = 1.1 [0.7, 1.5], $p < 0.001$) and $\delta^{15}N$ (mean estimates = 1.1 [0.5, 1.7], $p < 0.001$) were significantly lower in females for Scopoli's shearwater. Isotopic values of Cory's shearwater were similar between sexes (mean estimates = 0.2 [−0.2, 0.6], $p = 0.272$ and mean estimates = 0.4 [−0.1, 1.0], $p = 0.106$ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively), and in Cape Verde shearwater, isotopic values were significantly lower in females, only when considering $\delta^{15}N$ (mean estimates = 0.4 [−0.1, 0.9], $p = 0.112$ and mean estimates = 1.2 [0.4, 1.9], $p = 0.002$ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively). Mean $\delta^{15}N$ values for Cape Verde shearwaters were significantly higher than for the other species (mean estimates = 4.9 [3.5, 6.2], $p < 0.001$; Table S12).

The null model and the one including species best explained the Bayesian estimate of the standard ellipse area (SEAb) values. After performing model averaging, values of the SEAb differed among species—with Cory's shearwater presenting higher values, followed by Scopoli's shearwater—but not between sexes or among the size of core areas of the wintering distribution, with Scopoli's shearwaters showing the broadest isotope niches [mean estimates = 1.5 (0.9, 2.0)] (Tables S13 and S14).

4 | DISCUSSION

By combining geolocation data and isotopic values of feathers collected over 6 years, we evaluated the SS in spatio-temporal distribution, at-sea behavior, and feeding ecology in three closely related seabird species during their nonbreeding period. Migratory males of the three species arrived earlier than females at their breeding grounds, although differences were more subtle than expected (3 days earlier on average). Nonmigratory Cory's shearwater males remained in areas close to the colony in a larger proportion than females and arrived at the breeding colonies earlier than migratory males and both nonmigratory and migratory females, as was found in Catry et al. (2013). Such differences in migratory behavior can be explained by differential roles in reproduction according to the arrival time hypothesis, where the earlier arrival of males confers an advantage in mate acquisition and territory defense (Catry et al., 2013; Hedd et al., 2014; Kokko, Gunnarsson, Morrell, & Gill, 2006). Overall, males and females of the three *Calonectris* species did not differ in their spatial distribution and shared their main nonbreeding areas, except for a specific

TABLE 4 Linear mixed model testing for potential effects of bill size (residuals of the linear regression of PC1 scores as function of sex) and species in the stable isotope values of $\delta^{13}C$ (A) and $\delta^{15}N$ (B). (a) Structure of the candidate models evaluated to explain our data and their associated measures of information (AICc: Akaike's information criterion corrected; ΔAICc: AICc increments of each model in comparison with the best model; $\text{AICc}_{\text{weight}}$: AICc weights of each model in relation to the set of candidate models). The most parsimonious models and those models with ΔAICc < 2 are shown in bold. (b) Results of the mean estimates (and 95% confidence intervals in parentheses) with adjusted SE obtained after performing model averaging between the best-supported models with ΔAICc < 2. (c) Relative variance importance of the fixed effects obtained from model averaging. All the performed models included bird identity, year, and nonbreeding area as random effects

$\delta^{13}C$				$\delta^{15}N$			
(a) Fixed factors structure	**AICc**	**ΔAICc**	**$\text{AICc}_{\text{weight}}$**	**(a) Fixed factors structure**	**AICc**	**ΔAICc**	**$\text{AICc}_{\text{weight}}$**
Sex + Species +Sex:Species	**330.1**	**0.0**	**0.647**	**Sex + Species +Sex:Species**	**462.2**	**0.0**	**0.283**
Sex + Species + Bill size + Sex:Species	**331.9**	**1.8**	**0.260**	**Sex + Species +Bill size + Sex:Bill size**	**462.6**	**0.4**	**0.228**
Sex + Species +Bill size + Sex:Species + Sex:Bill size	334.0	3.9	0.091	**Sex + Species**	**463.0**	**0.8**	**0.191**
Sex + Species	343.2	13.1	0.001	**Sex + Species +Bill size + Sex:Species**	**463.4**	**1.3**	**0.150**
Sex + Bill size	344.1	14.0	0.001	Sex + Species +Bill size	464.6	2.4	0.086
Sex + Species +Bill size	345.4	15.3	0.000	Sex + Species +Bill size + Sex:Species + Sex:Bill size	465.3	3.1	0.059
Sex + Bill size + Sex:Bill size	345.5	15.4	0.000	Species + Bill size	473.0	10.8	0.001
Sex	345.9	15.8	0.000	Species	479.3	17.2	0.000
Sex + Species +Bill size + Sex:Bill size	346.5	16.4	0.000	Sex + Bill size	506.6	44.5	0.000
Species + Bill size	351.8	21.7	0.000	Sex + Bill size + Sex:Bill size	508.5	46.4	0.000
Species	365.1	35.0	0.000	Sex	538.4	76.2	0.000
Constant	368.4	38.3	0.000	Constant	554.7	92.5	0.000
Bill size	425.2	95.1	0.000	Bill size	596.3	134.1	0.000
(b) Fixed effects	**Estimates**			**(b) Fixed effects**	**Estimates**		
Males	−15.6 (−16.2, −15.1)			Males	14.0 (12.8, 15.3)		
Females	−15.8 (−16.3, −15.3)			Females	13.5 (12.3, 14.7)		
Scopoli's shearwater	0.7 (0.3, 1.2)			Scopoli's shearwater	−0.2 (−1.0, 0.5)		
Cape Verde shearwater	0.8 (−0.1, 1.6)			Cape Verde shearwater	4.9 (3.5, 6.2)		
Females:Scopoli's shearwater	−0.9 (−1.3, −0.5)			Females:Scopoli's shearwater	−0.6 (−1.2, 0.0)		
Females:Cape Verde shearwater	−0.2 (−0.8, 0.3)			Females:Cape Verde shearwater	−0.8 (−1.6, 0.1)		
Bill size	0.1 (−0.1, 0.2)			Bill size	0.1 (−0.1, 0.4)		
				Females:Bill size	−0.2 (−0.3, 0.0)		
c) Relative variance importance (%)				**c) Relative variance importance (%)**			
Sex	1.0			Sex	1.0		
Species	1.0			Species	1.0		
Sex:Species	1.0			Sex:Species	0.5		
Bill size	0.3			Bill size	0.4		
				Sex:Bill size	0.3		

wintering area of Cory's shearwater located NW of the Azores archipelago, apparently only used by males. Furthermore, males and females did not differ in their spatial distribution when sharing a given nonbreeding area (i.e., at medium geographical scale), which would exclude hypotheses related to social dominance occurring during this period. In all three species, males generally showed greater values of $\delta^{13}C$ and $\delta^{15}N$ compared to females, although such differences were not always statistically significant. Given that the distribution within each nonbreeding area did not differ between sexes, this result cannot arise from geographic differences in baseline isotopic levels, but suggests a subtle SS in trophic level and diet. However, we cannot be conclusive in this regard.

4.1 | Spatio-temporal segregation between males and females

We found some sexual differences in the timing of migratory movements in the three species and in the use of nonbreeding areas in Cory's shearwater. Only Cory's shearwater males from Vila, and a larger proportion of males than females from Veneguera, remained in areas close to their respective colonies year-round. Furthermore, males of the three species departed earlier than females from their breeding colonies in autumn at the onset of the postbreeding migration. In most cases, males also arrived earlier than females at the breeding colony, although this difference might vary depending on species, nonbreeding area, and year.

The intersexual differences we found in the nonbreeding distribution of Cory's shearwaters are similar to those previously found for the same species in the Selvagens Islands (Pérez et al., 2013). The social dominance hypothesis could explain these results, with individuals of the larger sex staying closer to the breeding grounds and forcing subordinates to migrate further away. However, in the Veneguera colony (Canary Islands), for which we had a larger sample size, some females also did not migrate and wintered in the Canary Current, near the breeding colony. Furthermore, all areas, except the area NW of the Azores, were shared by males and females and we found no segregation between sexes in the spatial distribution within each nonbreeding area for any of the species we considered. Similarly, Pérez et al. (2013) found no association between body size and the decision to migrate or remain resident in Cory's shearwater. Body size can be ruled out when explaining sexual differences in migration patterns, and our results, therefore, do not support the social dominance hypothesis for explaining the sexual differences observed in the use of the nonbreeding areas.

The arrival time hypothesis could explain both the greater tendency of Cory's shearwater males to remain resident and the slight, but consistent, phenological differences between sexes in the three species we studied. The early arrival of one sex at breeding grounds could be essential to ensure mating opportunities and the acquisition of suitable territories for breeding (Hedd et al., 2014; Ketterson & Nolan, 1983). The earlier arrival of males occurs in many migratory bird species, while the opposite has been observed in only a few sex-role-reversed bird species (Kokko et al., 2006; Reynolds, Colwell, & Cooke, 1986). In our study, sexual differences among migratory birds were more subtle than expected, since we found that migratory males arrived at breeding colonies only about 3 days earlier than migratory females on average. However, nonmigratory males arrived approximately 23 days earlier than migratory males, and about 5 days earlier than nonmigratory females, at their respective breeding colonies. Hence, despite the slight difference in the arrival dates among migratory birds, the pattern of males arriving at breeding colonies earlier than females has been consistent, being even more pronounced when males decide to remain resident. We suggest that the differences between migratory males and females are not so pronounced since the birds share the same nonbreeding areas to winter, and the latitudes of nonbreeding areas elected were related to the date of return to the breeding grounds. As previously observed in another study, the farther the shearwaters traveled from the colony, the later they returned to breed in the subsequent breeding period (Müller, Massa, Phillips, & Dell'Omo, 2015). In other studies, females wintered further south/north than males and returned approximately 5–10 days later to breeding colonies (Catry et al., 2005; Müller et al., 2014; Phillips et al., 2005). Furthermore, the earlier departure of males from colonies for the postbreeding migration can be facultative since shearwaters are not territorial at sea and there may be no advantage in arriving at the nonbreeding areas earlier than potential competitors (Kokko, 1999). However, our results are consistent with those of Müller et al. (2015), who have suggested that Scopoli's shearwater males leave the breeding areas earlier than females so they can arrive earlier in the subsequent reproductive season, in a kind of "domino effect" (Briedis et al., 2019). According to the "domino effect," the timing of one phase of the annual cycle may affect the timing of the subsequent phase (Briedis et al., 2019; Gow et al., 2019), in this case, between postbreeding migration and arrival at the breeding colony for the subsequent reproductive season. Furthermore, although both sexes contribute equally to incubation and chick rearing (Hamer, Schreiber, & Burger, 2002), males tend to spend more time and energy defending the nests at the beginning of the breeding period, which could also explain their earlier arrival (Werner et al., 2014; Hedd et al., 2014). Hence, sex differences in migration distance and timing may be better explained by the different roles in reproduction between males and females (Catry et al., 2005).

4.2 | Sexual differences in at-sea behavior and feeding ecology

Our results concerning at-sea behavior and feeding ecology could be considered consistent with the ecological specialization hypothesis. In the three species, δ^{13}C and δ^{15}N values of the S13 remige (molted during the nonbreeding season) were slightly higher in males than in females. In seabirds, sexual differences in isotope ratios are often documented during different stages of the breeding period, but do not necessarily remain consistent year-round (Phillips, Lewis, González-Solís, & Daunt, 2017; Phillips et al., 2011). The slight differences between sexes in δ^{13}C and δ^{15}N values found in our study suggest a small dietary segregation between sexes of the three species during the nonbreeding period. These variations may occur due to differences in the metabolic rates between males and females (González-Solís et al., 2000). However, the extent to which metabolic rates affect species with slight SSD, such as *Calonectris* shearwaters, is poorly known. We also recognize that other factors not considered in this study, such as age, may influence metabolic rates (Alonso et al., 2012). Furthermore, sexual differences in δ^{13}C and δ^{15}N values could reflect different S13 remige molting strategies among males and females, which occurs during the nonbreeding period (Ramos, Militão, et al., 2009c). Nevertheless, no differences were found in the onset of the molt of the primary remiges of Cory's shearwater males and females during the late chick-rearing period (Alonso et al., 2009), and further investigation into sexual differences in molting schedules is required.

Hence, we argue that at the end of the breeding period, when rearing duties are more relaxed and shearwaters can disperse over wider areas (Shaffer et al., 2006; González-Solís et al.,2007), foraging niches may better reflect intrinsic, sex-specific feeding preferences that may persist throughout the entire nonbreeding period (Clay et al., 2016).

Differences in carbon isotope ratios are frequently used to determine differences between terrestrial versus marine ecosystems, inshore versus offshore, and pelagic versus benthic food webs (Quillfeldt, McGill, & Furness, 2005). We did not detect a clear spatial segregation between males and females within each nonbreeding area; however, females make use of a greater core area (50% KUD) than males, which may suggest that males forage more efficiently than females (Weimerskirch, Cherel, Cuénot-Chaillet, & Ridoux, 1997), as females need to forage in a larger area than males to ensure their requirements. Furthermore, higher δ^{13}C values in males, particularly in Scopoli's shearwaters, may suggest that males feed more heavily on the benthic prey (with higher δ^{13}C values) available at the surface layer in more central areas of the upwelling systems, whereas females feed in more peripheral areas, probably taking advantage of lesser quality food resources, with lower δ^{13}C values. The diet of *Calonectris* shearwaters during the nonbreeding period is almost unknown (Barrett et al., 2007; Petry, Krüger, da Silva Fonseca, Brummelhaus, & da Cruz Piuco, 2009). In general, these shearwaters are shallow divers and tend to feed on surface prey during daylight (Cianchetti-Benedetti et al., 2017; Dias et al., 2012b; Grémillet et al., 2014; McNeil, Drapeau, & Pierotti, 1993), although both Scopoli's and Cory's shearwaters may also forage at night (Dias et al., 2012b; Rubolini, Maggini, Ambrosini, & Imperio, 2015). When in productive waters of nonbreeding areas, birds may make use of the sit-and-wait foraging strategy, and food availability may be improved by the activities of subsurface predators and fisheries (Péron et al., 2010; Phillips et al., 2017). The more intense activity at night among female *Calonectris* shearwaters may suggest that they take greater advantage of the diel vertical migration of some mesopelagic fish, crustaceans, and squids (lower trophic level prey characterized by lower δ^{15}N values) than males do (Hays, 2003; Spear et al., 2007). In addition, sexual differences in the at-sea activity patterns and in isotopic values may also result from males exploiting more fishery discards than females (Hobson, Piatt, & Pitocchelli, 1994; Ramos, González-Solís, et al., 2009b), which are often dominated by inshore benthonic species with higher δ^{13}C and δ^{15}N values (Bugoni, Griffiths, & Furness, 2011; Hobson et al., 1994). The interactions of Scopoli's shearwaters with longline fisheries increase when the density of the fleet of operating trawlers is lower (and consequently, less discards are available) in the western Mediterranean (Soriano-Redondo et al., 2016), confirming that fisheries modify the natural way in which seabirds look for resources. Furthermore, the bycatch of Scopoli's shearwaters by longline fisheries in this area is male-biased, especially during the prelaying period (Cortés, García-Barcelona, & González-Solís, 2018).

In sexually dimorphic species, we might expect sexual differences in diet to be the result of different body sizes and, in particular, different sizes of feeding structures, such as the bill in birds (Amadon, 1959; Selander, 1966). Males are larger than females in the three shearwater species considered in this study, particularly with respect to bill size. We found a slight effect of bill measurements on the isotopic differences between sexes, which may suggest that at least some males are capable of feeding on larger prey at higher trophic levels (i.e., with higher δ^{15}N values; Cherel & Hobson, 2005). Previous studies conducted on Cory's shearwaters concluded that SSD in bill and wing dimensions was poor predictors of the way males and females exploit the marine environment (Navarro et al., 2009; Ramos, Granadeiro, et al., 2009a). Thus, the role of sexual selection in sexual differentiation in bill size in *Calonectris* shearwaters remains unclear, and results suggest the need to investigate the effect of individual body and bill size once controlled for sex.

5 | CONCLUSIONS

In summary, Cory's shearwater males preferred to remain closer to the breeding grounds during the nonbreeding period compared to females. Sex-related differences in several parameters of the migration phenology were also found, with males leaving and arriving earlier than females at the breeding grounds. This could be attributed to differential reproductive roles, in particular to the greater involvement of males in nest defense, rather than to male social dominance. This was supported by the apparent absence of spatial segregation between males and females within all main nonbreeding areas, though this finding should be viewed with some caution due to the lack of fine-scale spatial resolution of the geolocators. Nevertheless, we observed some differentiation between sexes in nocturnal flight behavior, with males displaying more diurnal flying activity than females in general. This finding was supported by isotopic values, which could reflect differences in feeding preferences and diet composition. However, trophic segregation was not fully supported by the SSD in bill size. Overall, our study showed that SS in ecological niche in seabirds persists year-round consistently but at a different extent. Based on our findings, and the fact that most of the studies conducted during the breeding period have reported sexual differences in the stable isotope values, we hypothesized that males and females might have evolved in exploiting different ecological niches as a result of an ecological specialization derived from differential reproductive roles (rather than from social dominance), which may persist throughout the annual cycle.

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CONFLICT OF INTEREST

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AUTHOR CONTRIBUTIONS

FDF performed the molecular sexing, analyzed geolocator, and derived data, performed the statistical analyses, and drafted the manuscript; JMR-G conducted fieldwork, analyzed geolocator data, wrote the R code for spatial analyses, and reviewed the draft versions of the manuscript; TM conducted fieldwork, analyzed geolocator data, carried out stable isotope analyses, and reviewed the manuscript; JB, VCN, and DO conducted fieldwork and reviewed the manuscript; RR conducted fieldwork, analyzed geolocator data, provided advice in ecological issues, and reviewed the process of drafting the manuscript; and JG-S conceived the study, devised structure of the manuscript and data analysis pipeline, got funding, supervised the work, and reviewed the manuscript.

DATA AVAILABILITY STATEMENT

Tracking data are available at the BirdLife International Seabird Tracking Database (http://www.seabirdtracking.org) under the Dataset IDs: 974, 975, 976, 977, and 983. The data that support the findings of this study are openly available in the University of Barcelona (UB) Digital Repository (http://hdl.handle.net/2445/136898).

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